

**A synopsis of South American *Mycale* (*Mycale*) (Poecilosclerida, Demospongiae), with description of three new species and a cladistic analysis of Mycalidae**

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**A synopsis of South American *Mycale* (*Mycale*) (Poecilosclerida, Demospongiae), with description of three new species and a cladistic analysis of Mycalidae.** - Species of *Mycale* (*Mycale*) known so far from the coasts of South America are: *M. (M.) doellojuradoi*, *M. (M.) laevis*, *M. (M.) lapidiformis* and *M. (M.) quadripartita*. *M. (M.) arenaria* nom. nov. is proposed as a replacement name for *M. (M.) arenosa* Hajdu & Boury Esnault, 1991, preoccupied by *M. parasitica* var. *arenosa* Hentschel, 1911. *Esperella fusca* Ridley & Dendy, 1886 was found to be a junior synonym of *M. laevis*. Material of an additional three new species is here described: *M. (M.) beatrizae* n.sp., *M. (M.) darwini* n.sp. and *M. (M.) thielei* n.sp. (from SE Brazil, Galapagos and Chile respectively). Short descriptions are added for the previously known species, as well as an identification key to all of them. Some morphological characters of *Mycale* and the subgenus *Mycale* are discussed in a phylogenetic perspective - material of more than 110 species of the genus has been preliminarily evaluated for this purpose - and some suggestions of new lines of investigation are proposed. Finally, a cladistic analysis of phylogenetic relationships within the Mycalidae is presented.

**Key-words:** Demospongiae - Porifera - *Mycale* - South America - Systematics - Taxonomy - Anisochela - Phylogeny.

INTRODUCTION

"If, as I believe to be the case, the true object of classification should be the arrangement of individuals, species, genera, and so forth, in strict accordance with their phylogenetic relationships, it will be obvious ... that the sponge spicule must have a very high taxonomic value."

(DENDY, 1921: 53)

Both Pacific and Atlantic coasts of South America range among the least studied marine biotas, especially when marine sponge faunas are concerned (DE LAUBENFELS, 1956; BOURY-ESNAULT, 1973; HECHTEL, 1976; DESQUEYROUX-FAÚNDEZ & MOYANO, 1987; CUARTAS, 1991; HAJDU *et al.*, 1992; VAN SOEST, 1994). This article is focused on a conspicuous genus of marine Demospongiae, *Mycale*, distinguished on the basis of a singular combination of spicules, palmate anisochelae occurring along with mycalo-styles [(sub)(tylo)styles with faintly constricted neck and/or faintly swollen tyle, figs. 2, 10, 21, 23, 30, 44, 70; see also HAJDU *et al.*, 1994a]. Although there are more than 150 nominal species of *Mycale* worldwide (DOUMENC & LÉVI, 1987), the generally complex set of morphological characters of these species (e.g. up to eight categories of micro-scleres) tends to make their identification straightforward. Shortcomings are the overall poor quality of most earlier taxonomic descriptions and the lack of identification keys.

Material derived from relatively recent collections along both Pacific and Atlantic coasts of South America revealed three new species of *M.* (*Mycale*), and prompted us to start a revision of species belonging to the subgenus and occurring in the area. Taxonomic treatment of these revealed a whole set of morphological characters never discussed in a phylogenetic perspective before, and motivated us to advance some hypothesis of evolutionary trends within the genus *Mycale* stressing the need for a detailed assessment of shared spicular morphological features (RIDLEY & DENDY, 1887; DENDY, 1921; HAJDU *et al.*, 1994a) as the basis for a more consistent classification of the assemblage. This conclusion is derived from the observation of inconsistencies regarding shared ectosomal/choanosomal skeletal architectures, which constitute the basis of the currently used scheme for subgeneric/generic subdivision of *Mycale* (TOPSENT, 1924; VAN SOEST, 1984; BERGQUIST & FROMONT, 1988).

## MATERIALS AND METHODS

A revision of species assigned to *Mycale* is under way (Hajdu, in prep.), performed in one or more of the following ways: 1) reassessment of original descriptions, 2) compilation of data from several available descriptions for each species, 3) study of type material, and 4) study of additional specimens both published and unpublished, on loan from various institutions. More than 110 species of *Mycale* are represented by specimens (one or more, type or not) available to the authors.

Specimens from the Gulf of Ancud (Chile) were collected during an ecological survey undertaken by the Instituto de Zoología of the Universidad Austral de Chile, Valdivia, in 1971. The single specimen from Ubatuba (Brazil) was dredged during an oceanographic cruise of the N.O. "Prof. Besnard" of the Instituto Oceanográfico of the Universidade de São Paulo, and is part of a collection donated to the Porifera collection of the Departamento de Zoologia of the Universidade Federal do Rio de Janeiro (Brazil). The specimen from the Galapagos was collected during the SEPBOP project of the Smithsonian Institution (U.S.A.), and belongs to a large collection on loan to the Institute of Systematics and Population Biology of the University of Amsterdam (The Netherlands). Figure 1 shows the South American distribution of the species presently dealt with.

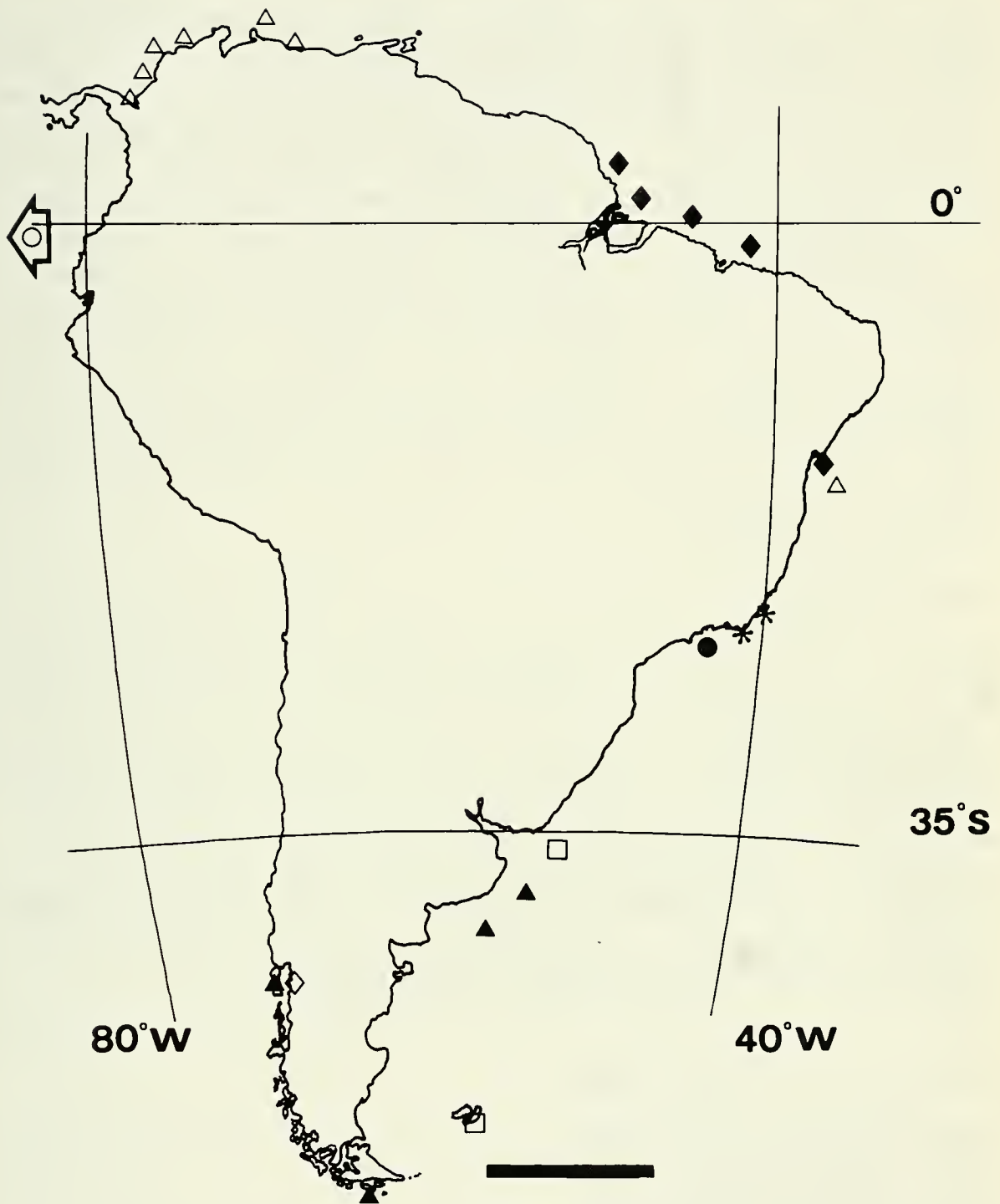


FIG. 1

Simplified map of South America showing occurrence of species of the subgenus *Mycale*. *Mycale (M.) arenaria* nom. nov. [\*]. *Mycale (M.) beatrizae* n.sp. [●]. *Mycale (M.) darwini* n.sp. [○]. *Mycale (M.) doellojuradoi* Burton, 1940 [▲]. *Mycale (M.) laevis* (Carter, 1882) [Δ]. *Mycale (M.) lapidiformis* (Ridley & Dendy, 1886) [□]. *Mycale (M.) quadripartita* Boury-Esnault, 1973 [◆]. *Mycale (M.) thielei* n.sp. [◇]. Scale = 1000 km.



Dissociated spicules slides and thick sections slides were made according to the usual widespread procedures (RÜTZLER, 1978). Spicules for SEM study were prepared in the same way, but vacuum coated and analysed partly in a Zeiss Digital Scan Microscope DSM 940 (MHNG) at an accelerating voltage of 20 Kv, and magnifications of up to 10000 times; partly in an I.S.I. ds 130 Scanning Microscope (University of Amsterdam) at an accelerating voltage of 10 to 15 Kv, and magnifications of up to 7000 times. Specimen sections for SEM were simply dried in a stove at 60°C for a few minutes (5-30) prior to vacuum coating.

Throughout this article the suffixes applied to microscleres are indicative of size, viz “-I” > “-II” > “-III”, but may also imply conjectures of homology. A step is made, which has never been made before, viz. a species with only two categories of a given microsclere may be described as bearing categories “-I” and “-III”. Such recognition is only possible by comparison with species bearing three categories of similarly shaped microscleres. Descriptions of anisochelae morphology make use, to a certain extent, of the terminology used by DENDY (1921), DOUMENC & LÉVI (1987) and HAJDU *et al.* (1994a).

The cladistic analysis performed here was undertaken on SWOFFORD'S (1990) program PAUP vs. 3.0.

Abbreviations used in the text are: BMNH (Natural History Museum, London), I.O.-USP (Instituto Oceanográfico, Universidade de São Paulo), MACN (Museo Argentino de Ciencias Naturales), MHNG (Museum d'histoire naturelle, Genève), MSNG (Museo Civico di Storia Naturale "Giacomo Doria", Genova), N.O. (Navio Oceanográfico), R.V. (Research Vessel), SEPBOP (Southeastern Pacific Biological Oceanographic Program), SMF (Natur-Museum Senckenberg, Frankfurt am Main), UFRJPOR (Universidade Federal do Rio de Janeiro, Porifera collection), USARP (United States Antarctic Research Program), USNM (United States National Museum, Smithsonian Institution, Washington D.C.), ZMA (Zoölogisch Museum, Amsterdam), ZMB (Museum für Naturkunde der Humboldt-Universität, Berlin), ZMH-S (Zoologisches Museum Hamburg, Porifera collection).

## SYSTEMATIC DESCRIPTIONS

Order Poecilosclerida Topsent, 1928

Suborder Mycalina Hajdu, Van Soest & Hooper, 1994.

Family Mycalidae Lundbeck, 1905

Genus **Mycale** Gray, 1867

(refer to WIEDENMAYER, 1989: 83-84 for a list of synonyms of the genus).

*Definition:* Mycalidae with anisochelae. Type species: *Hymeniacidon lingua* Bowerbank, 1866.

*Remarks:* Firm establishment of the monophyly of the Mycalidae is still wanting. This brings some uncertainties over the status of *Mycale* itself. HAJDU *et al.* (1994b) postulated the character chelae to be synapomorphic for the orders



Poecilosclerida and Haplosclerida, which makes its occurrence in the Mycalidae (*Esperiopsis* and a few *Mycale*) likely to be plesiomorphic. An alternative solution exists, however. If one considers the possibility that chelae might have been "switched-off" at the ancestor of the Desmacellidae-Hamacanthidae-Mycalidae clade (HAJDU, 1994), there would be two nodes before its possible "switch-on" in the Mycalidae, a condition taken as sufficient to postulate the derived condition of a character (MADDISON *et al.*, 1984). Accordingly, if isochelae are postulated to have been switched-on at the ancestor of the Mycalidae clade, the occurrence of anisochelae in *Mycale* is synapomorphic for the genus. However, under this scheme *Esperiopsis* can not be defined by possession of isochelae, as this character is hypothesized to be plesiomorphic at this level. BERGQUIST & FROMONT (1988) and HAJDU (1994) argued for the inclusion of *Esperiopsis* in the Mycalidae based on general skeletal resemblance, possession of mycalostyles [e.g. *E. villosa* (Carter, 1882), holotype examined BMNH 1882.7.28.55a], and ability to build rosettes [e.g. *E. radiata* (Topsent, 1927)]. The congruence of these characters makes it likely that the isochelae of *Esperiopsis* are homologous to the anisochelae of *Mycale*. It should be stressed that a few *Mycale* possess isochelae besides the usual complement of anisochelae [viz. *M. (Aegogropila) angulosa* (Duchassaing & Michelotti, 1864), *M. (A.) parishii* (Bowerbank, 1875)], and this may be suggestive of an alternative interpretation of affinities within the Mycalidae. If the ancestor of Mycalidae had originally aniso-, rather than isochelae, then *Esperiopsis* would be diagnosable by the change from aniso- to iso- condition. As a consequence *Mycale* would become paraphyletic, a strong argument toward raising monophyletic subgeneric assemblages to generic status (partly in agreement with BERGQUIST & FROMONT, 1988).

Furthermore, we must reckon with the fact that some *Mycale* completely lost their anisochelae complement. The existence of reduced specimens (= lacking some characters) has been observed in a few species, e.g. *M. (Carmia) microsigmatosa* Arndt, 1927 (see HAJDU & BOURY-ESNAULT, 1991). Further corroboration comes from VAN SOEST's (1984) suggestion of the likely synonymy of *Biemna microstyla* De Laubenfels, 1950 and *Desmacella meliorata* Wiedenmayer, 1977 to *M. (C.) microsigmatosa*; both former species were described without anisochelae. DE LAUBENFELS (1936) noted that reduced specimens are frequent within the polyphyletic Desmacidonidae Gray, 1872 [= Desmacididae Schmidt, 1870, see WIEDENMAYER (1989); see HAJDU (1994) and HAJDU *et al.* (1994b) for a discussion on the status of this assemblage].

A homoplastic origin of the aniso condition of the chelae is likely because of its occurrence in distant genera as *Iophon* Gray, 1867 (Microcionina); *Crella* Gray, 1867 and *Leptosiopsis* Topsent, 1927 (Myxillina); as well as in some supposedly more nearly related forms like *Asbestopluma* Topsent, 1901; *Cladorhiza* Sars, 1873 and *Corybas* (?) *lobata* (Bowerbank, 1866). Some taxa of uncertain relationships also possess palmate anisochelae, viz. *Phlyctaeuopora* Topsent, 1904 and *Acauthorhabdus* Burton, 1929. This picture makes it likely that several anisochelae are analogous, and apomorphic for several different clades in the poriferan hierarchy.

### Subgenus *Mycale* Gray, 1867

Type species: *Hymeniacidon lingua* Bowerbank, 1866.

*Diagnosis:* *Mycale* with a confused ectosomal skeleton of tangentially arranged megascleres over subectosomal divergent brushes. Toxas are always absent. Occasionally two categories of megascleres are found, in which case ectosomal and choanosomal ones may be distinguished by size alone (ectosomal ones slightly smaller), or additionally by a slight distinction in geometry (curved ectosomal ones vs. straight choanosomal ones). Surface pore-grooves may occur.

*Remarks:* The confused tangential ectosomal skeleton, the absence of toxas, anisochelae-III bearing a basal spur-like projection as well as anisochelae-I with a deeply-curved shaft (see descriptions below) are shared with the subgenus *Grapelia* Gray, 1867 and is indicative of their sister-group relationship. These points will be further discussed below.

### SYNOPSIS OF THE SPECIES OCCURRING ALONG THE COASTS OF SOUTH AMERICA

#### *Mycale* (*Mycale*) *arenaria* nom. nov.

*M. arenosa* HAJDU & BOURY-ESNAULT, 1991: 506; MURICY *et al.*, 1991: 1187, 1189-91; MURICY *et al.*, 1993: 429-430 (nec *M. parasitica* var. *arenosa* HENTSCHEL, 1911).

*M. fusca*; Solé-Cava *et al.*, 1981: 132 [nec *Esperella fusca* RIDLEY & DENDY, 1886; = *M. (M.) laevis* (CARTER, 1882), see below].

*Material studied:* Holotype, UFRJPOR 2431, 22°58'05"S-42°00'49"W (Praia do Forno, Arraial do Cabo, Brazil), 4 m deep, 28/IV/1988, coll. EH. Additional schizotypes: MHNG 993.123 and ZMA POR 8481. Paratypes: UFRJPOR 2432, 2433, 2434, 2435, Praia do Forno (Arraial do Cabo, Brazil), 3-4 m deep; UFRJPOR 2436, 2437, 22°58'51"S-42°00'34"W (Enseada, Arraial do Cabo, Brazil), 2 m deep; UFRJPOR 2438, Praia de João Fernandes (Búzios, Brazil), 3 m deep. Additional material: UFRJPOR 2439, 20°36'S-40°23'W, Três Ilhas (Guarapari, Brazil).

*Diagnosis:* This species can be distinguished from the only other *Mycale* (*Mycale*) with strongly curved anisochelae-I, two categories of megascleres and rare anisochelae-II - *M. (M.) darwini* n.sp. (see below) - by almost double the size of its choanosomal-megascleres and anisochelae-III.

*Description:* Specimens may be large (> 200 cm<sup>2</sup>; up to 5 cm thick). They are cushion-shaped with conical protuberances (up to 3 cm high) and bear pore-grooves on the irregular (detritus-covered) surface. Young sponges can be fistulose (up to 2 cm high by 1 cm in diameter), barely protruding from the substrate. The colour is bright-yellow to pale-orange, becoming light-brown in alcohol. Specimens are highly compressible and easily torn.

There is an ectosomal tangential skeleton composed of multiple layers of megascleres-II, just below which (or slightly intermingled) both rosettes of anisochelae-I (150 µm in diameter) and trichodragmas are abundant. Thick tracts of choanosomal-subtylostyles (> 4 mm at the base of the sponge) run toward the surface, branching and eventually anastomosing, and finally diverging into subectosomal brushes which support the tangential surface skeleton and may also trespass it.



Spicules (refer to HAJDU & BOURY-ESNAULT, 1991 for illustrations). Megascleres: Ectosomal-subtylostyles, fusiform, slightly curved, elliptic head faintly marked, apical extremity tapering gradually or slightly abruptly. Size: 323-440.8-588  $\mu\text{m}$  long and 4.4-11.5-16.8  $\mu\text{m}$  thick. Choanosomal-subtylostyles, fusiform, straight or slightly flexuous, elliptic heads faintly marked, apical extremity tapering gradually or slightly abruptly. Size: 546-645.5-754  $\mu\text{m}$  long and 6.9-12.3-17.3  $\mu\text{m}$  thick. Microscleres: Anisochelae-I (common), head, foot and space between them of about the same height, frontal ala of the head forms a larger angle with the shaft than does the one of the foot, shaft markedly curved. Size: 49.7-58.4-69.0  $\mu\text{m}$  long. Anisochelae-II (rare), robust, resembling anisochelae-I. Size: 40  $\mu\text{m}$  long. Anisochelae-III (uncommon), head higher than the rest of the microscelere, fusion of frontal and lateral alae of the head is variable, shaft bent at middle part, foot with a basal spur-like projection. Size: 17.2-26.8-40.9  $\mu\text{m}$  long. Sigmas (common), c-shaped, sharp extremities. Size: 28-35-43  $\mu\text{m}$  long. Trichodragmas (common). Size: 55-88.4-113  $\mu\text{m}$  long and 4.6-10.6-20  $\mu\text{m}$  thick.

*Remarks:* HENTSCHEL (1911) described *M. parasitica* var. *arenosa*. As he is clear in stating the subspecific rank of his specimen ("var."), the name *arenosa* becomes unavailable for subsequent use as a new name for *Mycale* (ICZN, 1985: Art. 45g, 52b, 53c). Accordingly, *M. (M.) arenaria* nom. nov. is here proposed as a replacement name for *M. (M.) arenosa* Hajdu & Boury Esnault, 1991.

*M. (M.) darwini* n.sp. and *M. (M.) paschalis* Desqueyroux-Faúndez, 1990, have anisochelae-I (curved) and -III (with a basal spur) which are comparable in shape to those of *M. (M.) arenaria* nom. nov. [figs. 15-17; DESQUEYROUX-FAUNDEZ (1990), figs. 40-41; cf. below, under "Remarks" to *M. (M.) darwini*; HAJDU & BOURY-ESNAULT (1991), figs. 6-10]. *M. (M.) thielei* n.sp. has only anisochelae-I conforming to the pattern in this group (see below). The interpretation of the significance of this shared trait is depending on a detailed analysis of relationships within the subgenus *Mycale*, because similar chelae occur in several species worldwide. *M. (M.) darwini* n.sp. differs from *M. (M.) arenaria* nom. nov. mainly by the much smaller size of its subtylostyles, anisochelae-III and sigmas. *M. (M.) paschalis* and *M. (M.) thielei* n.sp. differ by the possession of only one category of subtylostyles.

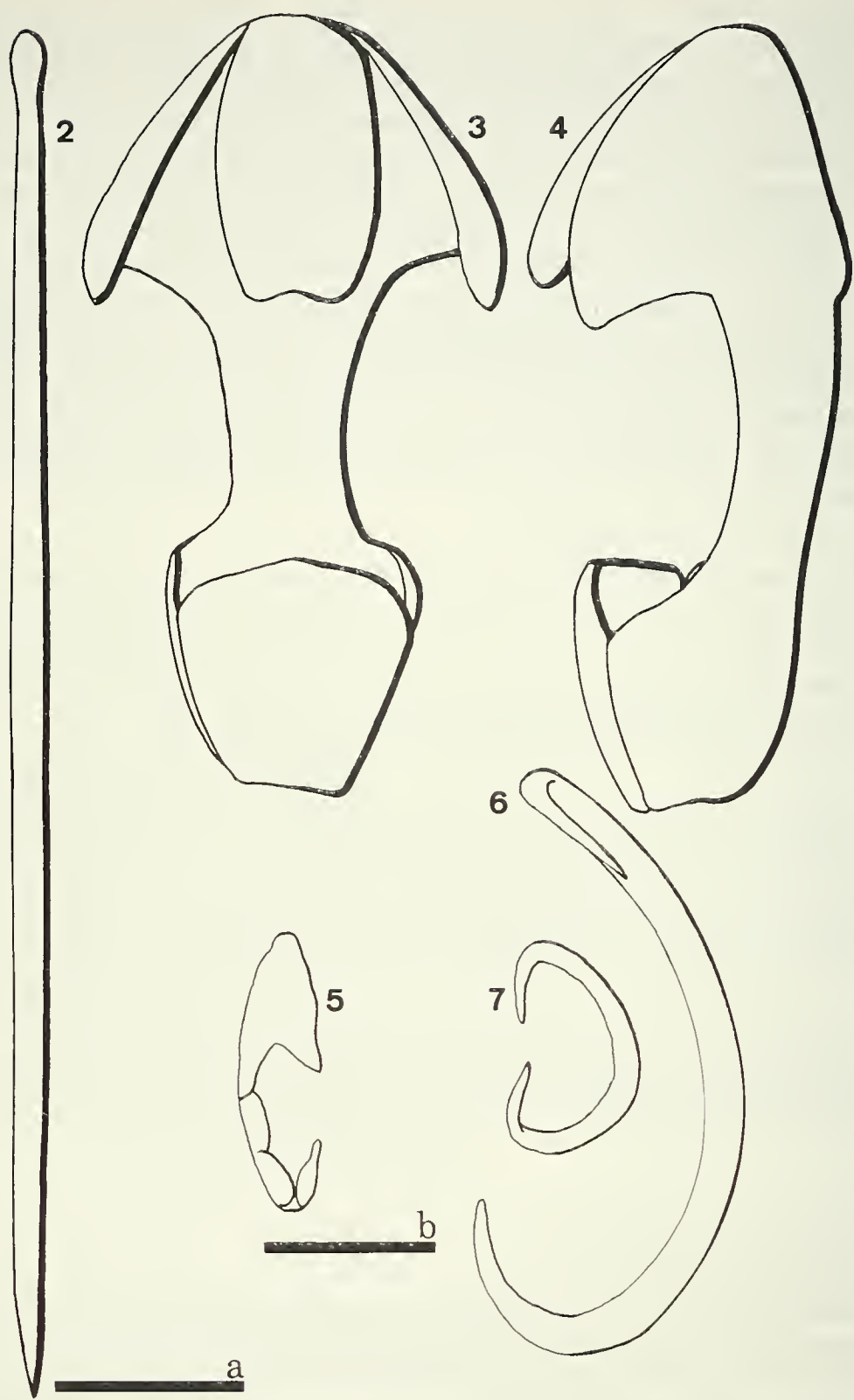
### ***Mycale (Mycale) beatrizae* n.sp.**

Holotype, UFRJPOR 4244, 24°09'0"S-44°22'5"W (Ubatuba, Brazil), stn. 5170, coll. Paulo Yukio, 136 m deep, coll. N.O. "Prof. Besnard" (I.O.-USP). Schizotypes under MHNG 993.122 (dissociated spicules mount) and ZMA POR 10656 (thick sections mount).

*Diagnosis:* The species is diagnosed as the only *Mycale (Mycale)* with anisochelae-I bearing a markedly curved shaft, large angle between this and the frontal ala of the head, and length never larger than 50  $\mu\text{m}$ .

*Description:* The specimen consists of a very small (8 x 10 mm) crust covering a piece of calcareous substrate. Its colour in the fixative is light grey.





FIGS 2-7

*Mycale (M.) beatrizae* n.sp. 2. subtylostyle. 3. frontal view of anisochela-I. 4. profile view of anisochela-I. 5. profile view of anisochela-III. 6. sigma-I. 7. sigma-II. Scale "a" (megascere) = 50  $\mu$ m. Scale "b" (microsceres) = 10  $\mu$ m.

The only part of the skeleton made out from the thick sections obtained is the ectosome which is constituted of an irregular network (halichondrioid reticulation) of tangentially laying megascleres, where intermingled rosettes of anisochelae-I (90-95  $\mu\text{m}$  in diameter) are common. Sigmas-II are very abundant at the surface.

**Megascleres:** Subtylostyles (fig.2), fusiform, straight or slightly flexuous, head only very faintly marked, apical termination most commonly tapering gradually. Size: 284-360.0-384  $\mu\text{m}$  long and 8-10-12  $\mu\text{m}$  thick. **Microscleres:** Anisochelae-I (common; figs. 3-4), robust, head only slightly higher than foot; frontal tooth of the head forms a larger angle with the shaft than does the one of the foot. Size: 38-40-44  $\mu\text{m}$  long. Anisochelae-II (very rare), frontal tooth of the head forms a larger angle with the shaft than does the one of the foot, shaft slightly bent inward at the terminaing point of the head's frontal ala, small space ( $\pm 3 \mu\text{m}$ ) between facing portions of both frontal alae. Size: 25-27  $\mu\text{m}$  long. Anisochelae-III (common; fig. 5), frontal alae of both extremities form a small angle with the slightly curved shaft, no basal spur-like projection on foot. Size: 16-17-20  $\mu\text{m}$  long. Sigmas-I (uncommon; fig. 6), slender, s- or c-shaped, gradually tapering extremities. Size: 36-40-44  $\mu\text{m}$  long. Sigmas-II (common; fig. 7), fragile, regularly s-shaped with gradually tapering extremities. Size: 12-15-16  $\mu\text{m}$ .

**Etymology:** The species is named for Beatriz Mothes in recognition of her contribution to our knowledge of the Brazilian marine sponges.

**Remarks:** The species seemingly closest to *M. (M.) beatrizae* n.sp. is *M. (M.) doellojuradoi*. Although both species differ by the presence of two categories of sigmas in the former versus none in the latter, as well as by small differences in the size of their spicules, there are undeniable similarities regarding the shape of the anisochelae-I and -III which are very likely to be homologous and indicative of close relationships.

### **Mycale (Mycale) darwini** n.sp.

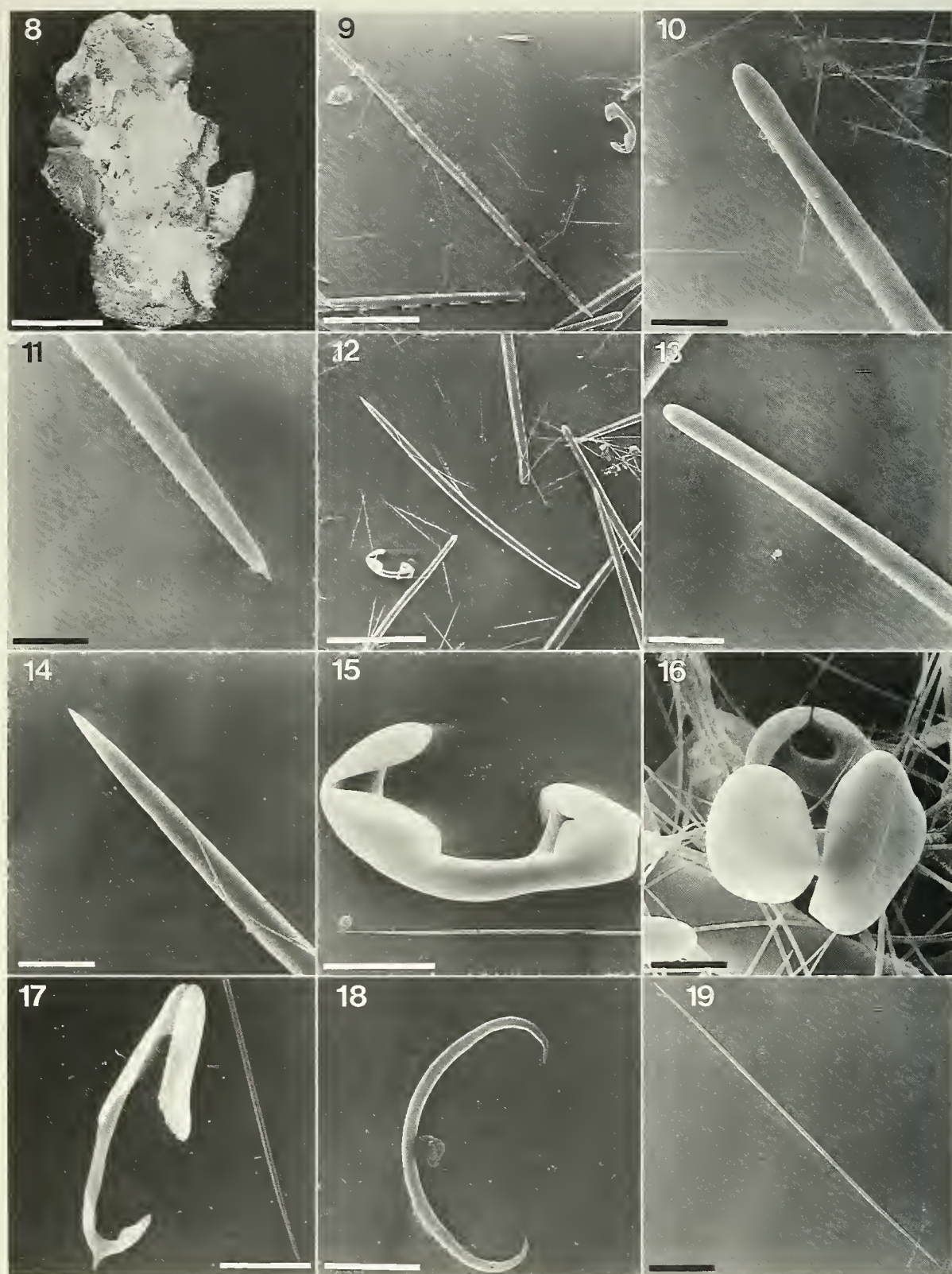
Holotype, USNM 43206, 00°12'S-90°51'W (Galapagos, Ecuador), 23/IX/1966, 34 m deep, coll. "Anton Bruun" (SEPBOPEX Exp., cruise 18b, # 794-e, Smithsonian Institution, U.S.A.). Schizotypes under MHNG 966.204 and UFRJPOR 4245 (dissociated spicules mounts), and ZMA POR 10655 (thick sections mount).

**Diagnosis:** This is the only species in the subgenus possessing two categories of megascleres which are smaller than 400  $\mu\text{m}$ .

**Description:** The specimen is a thin and hispid crust (20 x 9 mm) in the cavity of a small piece of volcanic rock (fig. 8). Colour in alcohol is very light brownish-yellow. Shallow pore-grooves can be seen on its surface.

The ectosomal tangential skeleton of megascleres is 120  $\mu\text{m}$  thick. The choanosome is very dense and tracts of megascleres (30-80  $\mu\text{m}$  thick) are seen in no distinguishable pattern, probably due to the incrusting aspect of the sponge. Subectosomal brushes are conspicuous however, lying side-by-side and projecting well beyond ( $\pm 300 \mu\text{m}$ ) the surface. Rosettes of anisochelae-I (100-120  $\mu\text{m}$  in diameter) are common in the subectosomal area. Other microscleres are common in the deeper parts of the thin choanosome.





FIGS 8-19

*Mycale (M.) darwini* n.sp. 8, holotype encrusting a fragment of volcanic rock. 9, choanosomal-subtylostyle. 10, head of choanosomal-subtylostyle. 11, sharp apex of choanosomal-subtylostyle. 12, ectosomal-subtylostyle. 13, head of ectosomal-subtylostyle. 14, sharp apex of ectosomal-subtylostyle. 15, profile view of anisochela-I. 16, top view of anisochela-I. 17, anisochela-III. 18, sigma. 19, raphid. Scales: fig. 8 = 1 cm; figs. 9 and 12 = 100  $\mu$ m; figs. 10-11 and 13-15 = 20  $\mu$ m; figs. 16 and 19 = 10  $\mu$ m; figs. 17 and 18 = 5  $\mu$ m.



Megascleres: Choanosomal-subtylostyles (figs. 9-11), fusiform, straight or slightly flexuous, elliptic head very faintly marked, apical termination tapering gradually. Size: 332-374.2-397  $\mu\text{m}$  long and 8-9.9-13  $\mu\text{m}$  thick. Ectosomal-subtylostyles (figs. 12-14), fusiform, slightly curved on the basal third, elliptic head faintly marked, apical termination tapering gradually. Size: 263-301.3-324  $\mu\text{m}$  long and 7.6-9.5-12  $\mu\text{m}$  thick. Microscleres: Anisochelae-I (common; figs. 15-16), head and foot of comparable height, frontal ala of the head forming a larger angle with the curved shaft, space between head and foot about 1/3 of microscle's length. Size: 50-53.5-58  $\mu\text{m}$  long. Anisochelae-III (common; fig. 17), fragile, frontal alae of both extremities forming same angle with shaft, head 1/2 microscle's length, foot vestigial, bearing basal spur-like projection. Size: 12-14.1-15  $\mu\text{m}$  long. Sigmas (common; fig. 18), fragile, slightly s-shaped; tapering gradually on both extremities. Size: 12-13.5-24  $\mu\text{m}$  long. Rhaphids (abundant; fig. 19), smooth; straight, tapering gradually. Size: 60-66.6-72  $\mu\text{m}$  long. Trichodragmas (uncommon), straight, thicker at middle part. Size:  $\sim$  68  $\mu\text{m}$  long and 7.4  $\mu\text{m}$  thick.

*Etymology*: The species is named after Charles Darwin and his contribution to the knowledge of the natural history of the Galapagos Islands.

*Remarks*: *Mycale* (*M.*) *darwinii* n.sp. seems close to *M.* (*M.*) *paschalis* (holotype reexamined: MHNG 985.938) on the basis of the shape of anisochelae-I and -III. *M.* (*M.*) *paschalis* was found to possess three categories of anisochelae, the smaller of which, overlooked by DESQUEYROUX-FAÚNDEZ (1990), has a spur-like projection too. The occurrence of sigmas in *M.* (*M.*) *paschalis* is doubtful, as those few observed were each of a different shape, although in the same size range (14-24  $\mu\text{m}$ ) as the ones in *M.* (*M.*) *darwinii* n.sp., suggesting that they may be contaminants. Differences between both species are the absence of anisochelae-II and the presence of two categories of megascleres of much smaller length ( $< 400 \mu\text{m}$ ) in *M.* (*M.*) *darwinii* n.sp., as opposed to three categories of chelae and only one much larger category of megascleres ( $> 600 \mu\text{m}$ ) in *M.* (*M.*) *paschalis*. Affinities with *M.* (*M.*) *arenaria* nom. nov. and *M.* (*M.*) *thielei* n.sp. are also likely (see above).

### **Mycale (Mycale) doellojuradoi** Burton, 1940

*M. doellojuradoi* BURTON, 1940: 104, pl. VIII; SARÀ, 1978: 40.

*Material studied*: Schizotype from holotype, BMNH 1933.6.10.112 (fragment from MACN 16241), 38°52'S-56°20'W (off Mar del Plata, Argentina), XII/ 1925, coll. "Undine" (fragment under UFRJPOR 3924); schizotype from paratype, BMNH 1933.6.10.111 (fragment from MACN 18521), 39°55'S-57°50'W (south of Mar del Plata, Argentina), 1929, 93 m deep, coll. "Maneco" (fragment under UFRJPOR 3923). Additional material: MHNG 987.471, Vald. 55, 42°30'S-73°46'W (Estero Castro, Chiloé, Chile), III/1987, 8 m deep (fragments under UFRJPOR 4229 and ZMA POR 10657).

*Diagnosis*: This is the only species in the subgenus with megascleres smaller than 500  $\mu\text{m}$  and no sigmas and/or raphids.

*Description* of the Chilean specimen: The sample is composed of two macerated fragments (83 mm x 23 mm x 23 mm; 89 mm x 29 mm x 29 mm). They are

fibrous, crumb-of-bread like, and easily torn (fig. 20). Stout reticulated spiculo-fibres project well beyond the surface of their supposedly apical part. The fragments are embedded by abundant polychaete tubes. There is a detachable surface peel in parts of the fragments.

The ectosomal skeleton is a loose and confused tangential reticulation of megascleres. It is 160-200  $\mu\text{m}$  thick on transverse sections. Rosettes of anisochelae-I are found mainly below the surface skeleton (a few ones deep in the choanosome are regarded artifacts due to dragging during slicing of the specimen) and have 110-120  $\mu\text{m}$  in diameter. The choanosomal skeleton is made up of ascending tracts of megascleres (80-160  $\mu\text{m}$  thick) which are mostly curved. These tracts end in divergent brushes which support the ectosomal skeleton without trespassing it. There are no large subectosomal spaces, rather, the choanosome is filled with organic matrix and embryonic stages intermingled with loose megascleres. Anisochelae-II and -III occur all over the sponge.

Megascleres: Subtylostyles (fig. 23), fusiform, mostly slightly flexuous, base only very faintly enlarged and oval in appearance, apical termination tapering gradually. Size: 373-404.2-433  $\mu\text{m}$  long and 3.6-8.0-10  $\mu\text{m}$  thick. Microscleres: Anisochelae-I (common; fig. 25), head only slightly higher than foot; frontal ala of the head forms a larger angle with the curved shaft than the one of the foot. Size: 50-53.1-58  $\mu\text{m}$  long. Anisochelae-II (common; fig. 26), head double height of foot, frontal alae of both head and foot forming a small angle with the straight shaft, frontal ala of the foot possesses a conspicuous cylindrical projection on its upper end parallel to the shaft. Size: 30-33.8-40  $\mu\text{m}$  long. Anisochelae-III (common; fig. 28), frontal alae of both extremities form a small angle with the slightly curved shaft, no basal spur-like projection on foot. Size: 17-20.0-24  $\mu\text{m}$  long.

*Remarks:* The specimen from Estero Castro (Chile) conforms in every smaller detail to the type specimens of *M. (M.) doellojuradoi* (figs. 21-22, 24, 27, 29) from the Argentinian Coast. SARÀ's (1978) record of the species from Ushuaia (Tierra del Fuego, Argentina) was already indicative of its austral affinities, which made its finding in Chile predictable. The species seems to be close to *M. (M.) beatrizae* n.sp. (see above).

### ***Mycale (Mycale) laevis* (Carter, 1882)**

*Esperia laevis* CARTER, 1882: 291

*Esperella fusca* RIDLEY & DENDY, 1886: 339; 1887: 72 [not *M. fusca* sensu SOLÉ-CAVA *et al.*, 1981; = *M. (M.) arenaria* nom. nov. see above].

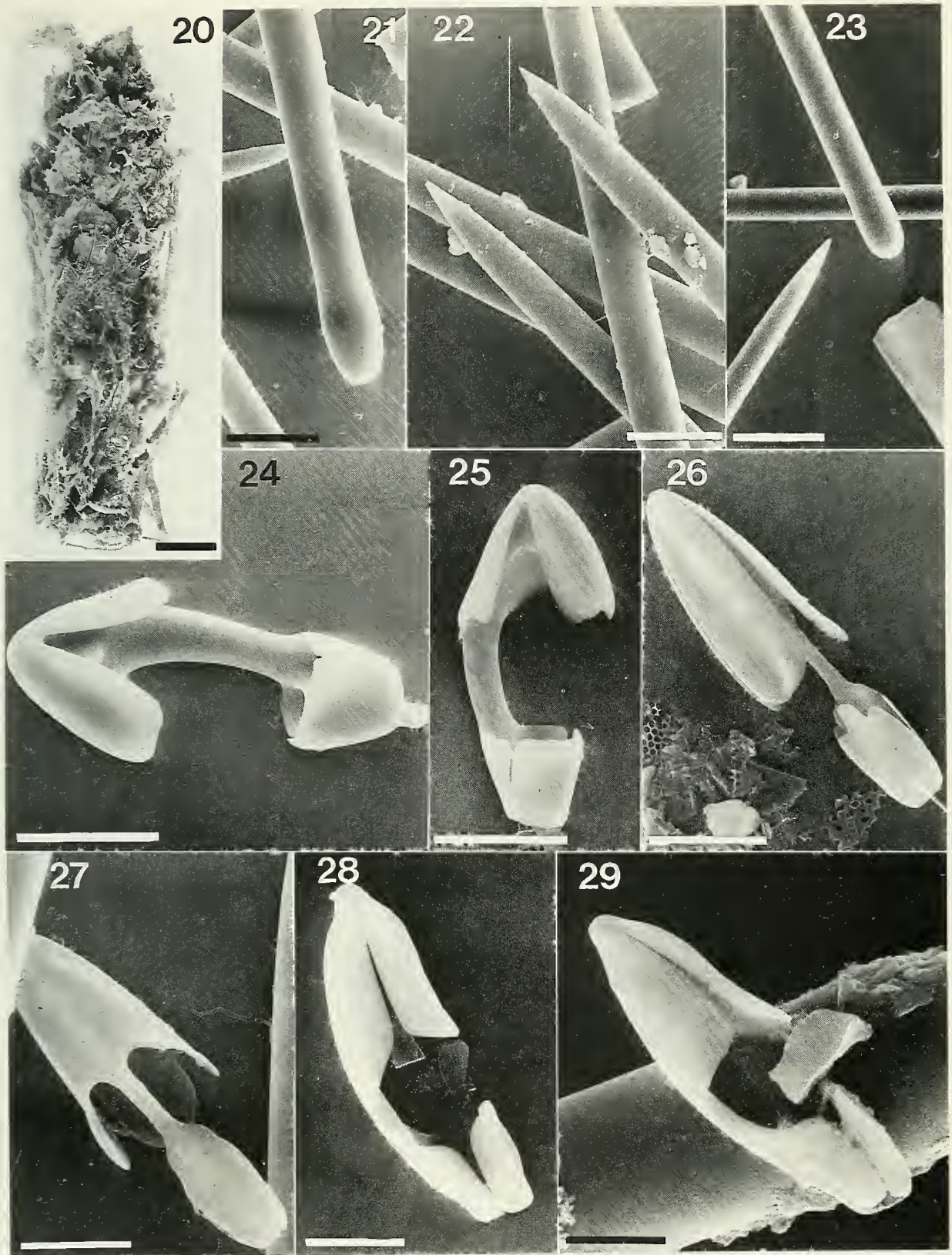
*M. laevis*; DE LAUBENFELS, 1936: 116; HECHTEL, 1965: 46; WINTERMANN-KILIAN & KILIAN, 1984: 132; WIEDENMAYER, 1977: 258; ALCOLADO, 1980: 4; PULITZER-FINALI, 1986: 125.

*M. (M.) laevis*; VAN SOEST, 1981: 12; 1984: 14; ZEA, 1987: 136.

*Oxymycale strongylata* PULITZER-FINALI, 1986: 134.

*Material studied:* Holotype, BMNH 1939.3.24.23 (fragment from the Liverpool Free Museum), Puerto Cabello ("Argo" Exp., Venezuela). Additional material: ZMAPOR 3331, Punta Guaniquilla (Cabo Rojo, Puerto Rico), 6 m deep, 16/XII/1963, coll. J.H. Stock (P.R.77);





FIGS 20-29

*Mycale (M.) doellojuradoi* Burton, 1940. 20, specimen from Estero Castro (Chile; MHNG 987.471). 21, head of subtylostyle from holotype. 22, apex of subtylostyle from holotype. 23, terminations of subtylostyles from the Chilean specimen. 24, profile view of anisochela-I from holotype. 25, profile view of anisochela-I from the Chilean specimen. 26, frontal view of anisochela-II from the Chilean specimen. 27, backside view of anisochela-II from holotype. 28, profile view of anisochela-III from Chilean specimen. 29, profile view of anisochela-III from paratype. Scales: fig. 20 = 1 cm; figs. 21-25 = 20  $\mu$ m; figs. 26 and 27 = 10  $\mu$ m; figs. 28 and 29 = 5  $\mu$ m.



ZMAPOR 4608, Awa Blancu (Curaçao), 10-20 m deep, underneath *Agelas*, 29/XII/1980, coll. R.W.M. van Soest; ZMAPOR 4609, 300 m SE Hilton Hotel (Curaçao), 10-12 m deep, among *Madracis*, 17/XII/1980, coll. R.W.M. van Soest. *Esperella fusca* - holotype, BMNH 1887.5.2.189, off Bahia ("Challenger" Exp., Brazil), 31 m deep. Schizotype, UFRJPOR 3494.

*Diagnosis:* *M. (M.) laevis* is the only species in the subgenus with two categories of anisochelae, generally smaller than 100 µm, where the smaller ones have a basal spur-like projection; one category of sigmas with a variable size, and one category of trichodragmas which are generally very abundant.

*Description* (emended from HECHTEL, 1965; VAN SOEST, 1984 and ZEA, 1987; along with field observations by EH in Belize): Cushion-shaped, a few milimeters to some centimeters thick. Massive-lobate or digitate specimens also occur and can reach enormous dimensions (> 50 cm long and 5-10 cm thick). Colour most frequently yellow or yellowish-orange, but rare yellow-green and pale whitish-yellow (cream) specimens occur. Compressible, spongy consistency, and smooth but uneven surface. Oscules up to 10-15 mm in diameter even on thinner reef specimens, characteristically encircled by a membranous fringe supported by longitudinally-running spicular tracts (50-600 µm thick), visible to the naked-eye.

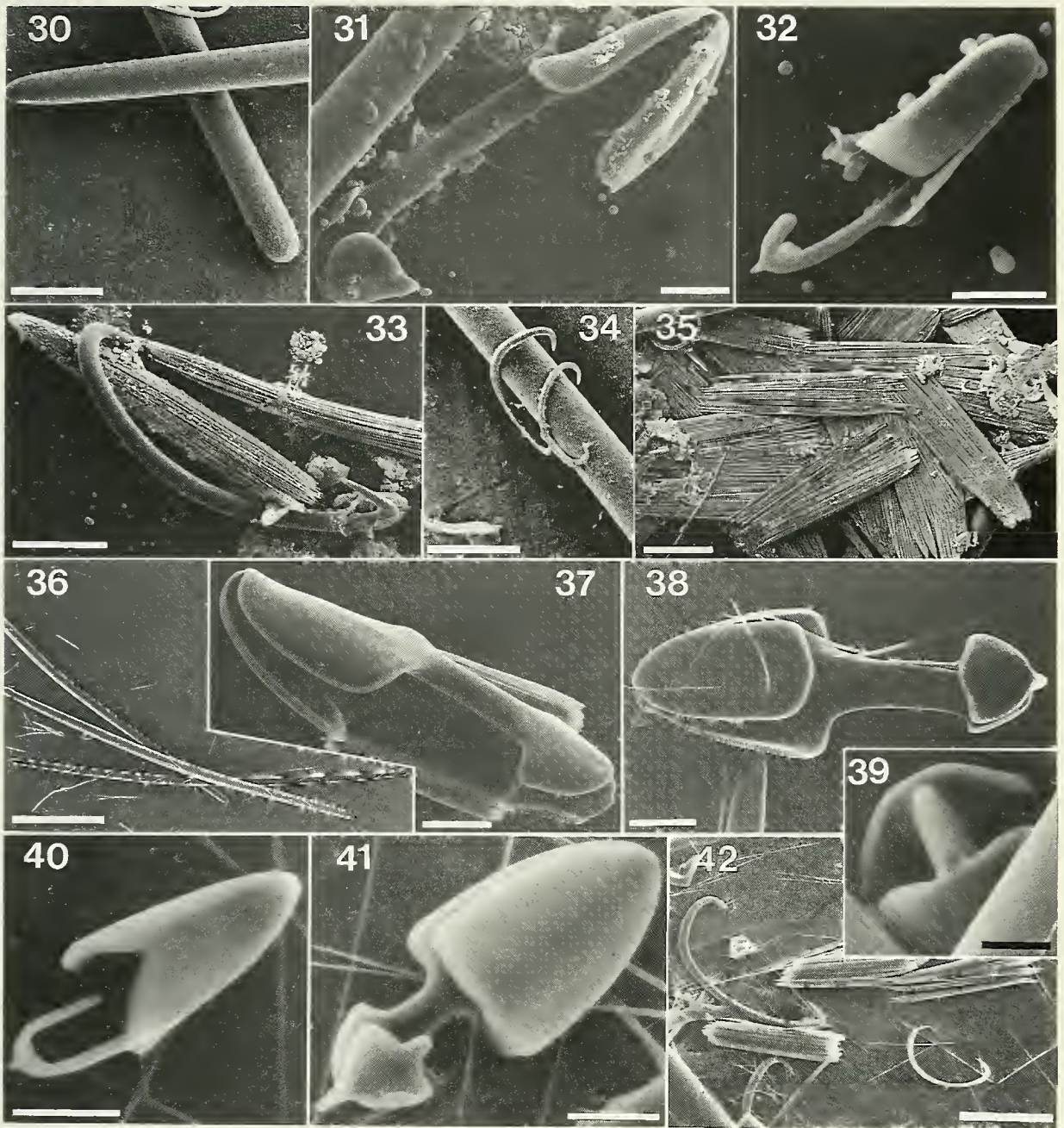
Ectosomal skeleton, a variably thick, variably dense tangential layer of subtylostyles strewn in a confused pattern. The choanosomal skeleton is composed by

TABLE 1

Spicule micrometries of *Mycale (M.) laevis* (Carter, 1882), *Esperella fusca* Ridley & Dendy, 1886 and *Oxymycale strongylata* Pulitzer-Finali, 1986, partly from the literature, partly remeasured. Micrometries refer to minimum-mean-maximum. Unless otherwise stated, N = 20 for material presently remeasured.

	subtylostyles length X width	anisochelae -I/-III	sigmas	trichodragmas
CARTER, 1882	479.2 X 12.5	75/ 20.8	41.7	66 X 7
presently remeasured	419-470.1-519 X 9-10.5-13	76 (N = 1)/ 19-20.5-23	102 (N = 1)/ 20-30.0-43	65-75.8-88 X 5-11.3-22
HECHTEL, 1965	377-596 X 7-18	57-100/ 15-28	17-77	50-70 X 10
VAN SOEST, 1984	475-570 X 7-17	68-75.7-84/ 18-21.6-24	12-23.4-34	52-61.8-72 X 5-7-9
PULITZER-FINALI, 1986 as <i>M. laevis</i>	470-580 X 10-16	59-78/ 16-21	18-46	50-81
ZEA, 1987	450?-552.1-619 X 9.0-15.2-23.3	71-76.0-90/ 17-20.6-26	6.9-25.4-56	55-57.5-76
RIDLEY & DENDY, 1886 as <i>E. fusca</i>	455 X 12.6	63/ not given	44	30 X 6.3
presently remeasured	318-357.5-398 X 8.8-10.6-13.2	53-57.6-62/ 15-18.0-23	17.6-33.8-41.8	25-29.9-35 X 5-6.4-9
PULITZER-FINALI, 1986 as <i>O. strongylata</i>	420-550 X 10-16	69-80/ 16-21	14-41	35-57





FIGS 30-42

*Mycale* (*M.*) *laevis* (Carter, 1882; holotype, BMNH 1939.3.24.23). 30, terminations of subtylostyles. Note almost strongyloid condition. 31, profile view of anisochela-I. Note almost straight shaft. 32, frontal view of anisochela-III. Note absence of alae on the foot and presence of basal spur. 33, rare unusually large sigma. 34, normal sigmas. 35, patch of trichodragmas. Scales: figs. 30 and 33-34 = 20  $\mu$ m; fig. 31 = 10  $\mu$ m; fig. 32 = 5  $\mu$ m; fig. 35 = 30  $\mu$ m. *Esperella fusca* Ridley & Dendy, 1886 (holotype, BMNH 1887.5.2.189). 36, subtylostyles. Note almost strongyloid shape. 37, profile view of anisochela-I. 38, frontal view of anisochela-I. 39, bottom side view of foot of anisochela-I. 40, profile view of anisochela-III. Note absence of alae on the foot and presence of basal spur. 41, uncommon highly developed form of anisochela-III bearing alae on the foot and two spurs. 42, sigmas and trichodragmas. Scales: fig. 36 = 100  $\mu$ m; figs. 37-38 = 10  $\mu$ m; figs. 39-41 = 5  $\mu$ m; fig. 42 = 20  $\mu$ m.



longitudinally-running tracts of subtylostyles, branching or anastomosing, which end in slightly divergent subectosomal brushes supporting the ectosomal tangential skeleton. Rosettes of anisochelae-I are common at the level of the brushes. Megascleres of variable thickness are scattered among the tracts giving the architecture a slightly confused appearance, more evident the closer to the sponge base. Trichodragmas, single or in clusters, as well as single raphides and sigmas occur throughout the sponge.

Spicules (micrometries see Table 1). Megasclere: (Subtylo)styles or (subtylo)strongyles (fig. 30), straight or slightly curved, thicker at central portion, abruptly pointed, sharp or roundish apex. Microscleres [semi-quantitative data based on very small fragment (8 X 5 X 1 mm) from the dry holotype, likely to be devoid of surface layer]: Anisochelae-I (rare; fig. 31), shaft mostly straight, forming rosettes. Anisochelae-III (uncommon; fig. 32), with basal spur-like projection. Sigmas (common; 33-34), c- or s-shaped, tapering gradually. Trichodragmas (abundant; 35).

*Remarks:* *Esperella fusca* is presently considered to be a junior synonym of *M. (M.) laevis* based on the overall shape of its spicules (figs. 36-42), which, nevertheless, are generally smaller than those of *M. (M.) laevis*.

*Oxymycale strongylata* Pulitzer-Finali, 1986 (holotype examined MSNG 47698) is also confidently assigned to *M. (M.) laevis*, due to the common occurrence of similar anisostongyles in the type specimen of the latter, as well as for the major resemblance of their microsclere complement [compare PULITZER-FINALI'S (1986), fig. 57, with figs. 30-35 in the present article].

### **Mycale (Mycale ?) lapidiformis** (Ridley & Dendy, 1886)

*Esperella lapidiformis* RIDLEY & DENDY, 1886: 338; 1887: 64, pl. XV, figs. 2, 10, 10a, pl. XVI, 2, 2a, 2b.

*M. lapidiformis*; BURTON, 1932: 289.

? *M. gaussiana* HENTSCHEL, 1914: 61-62, pl. V, fig. 9.

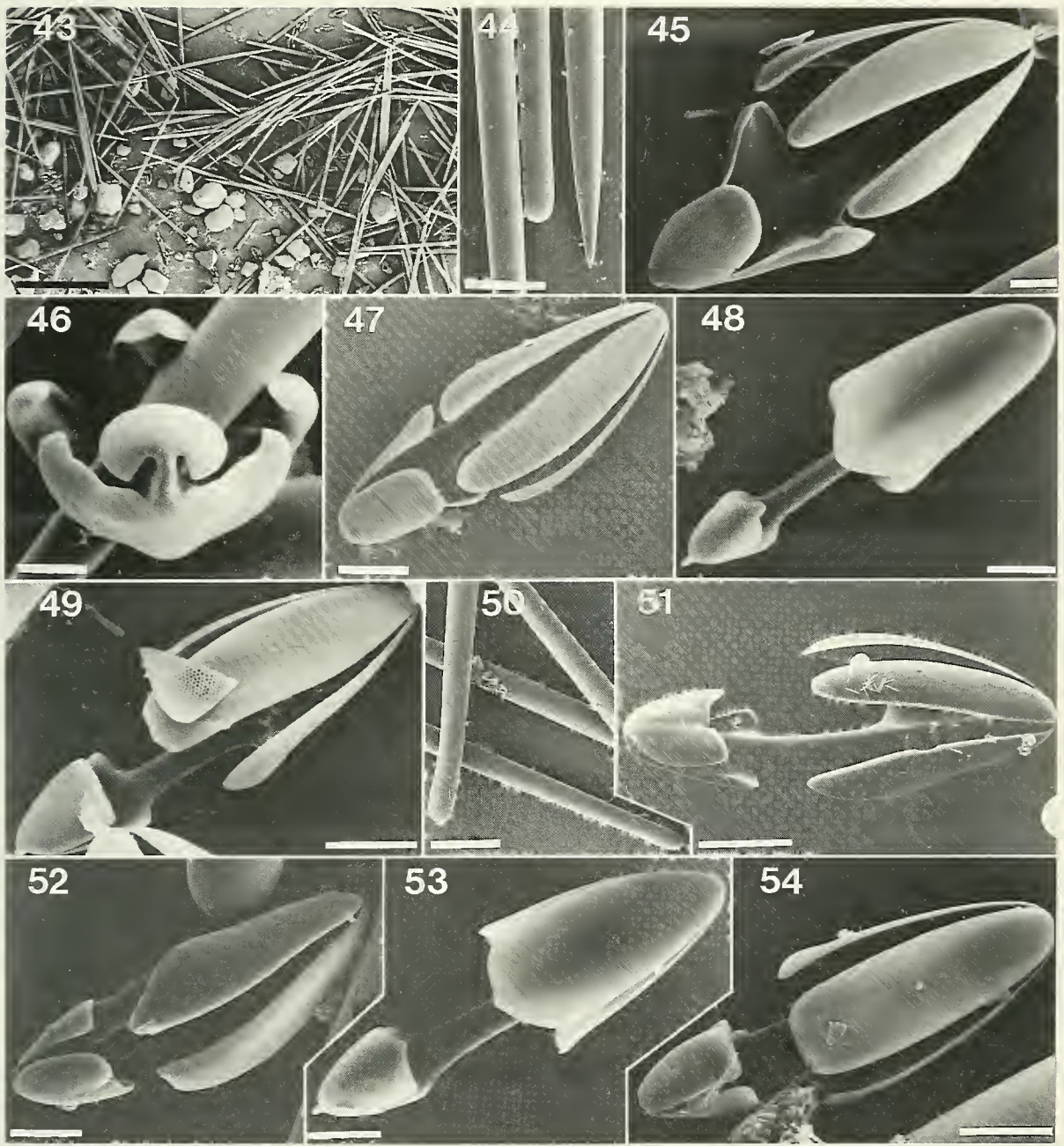
? *M. profunda* KOLTUN, 1964: 31, fig. 5.

*Material studied:* Holotype of *E. lapidiformis*, BMNH 1887.5.2.160, 37°17'S-53°52'W ("Challenger" Exp., Stn. 320, off the mouth of the Rio de la Plata), 14/II/1876, 1080 m deep, bottom of green sand. Schizotypes, UFRJPOR 5000 and ZMA POR 10658. Additional material: BMNH 1928.2.15.452, 52°40'S-58°30'W ("Discovery" Exp., Stn. W.S. 248, Falkland Islands), 20/VII/1928, 210-242 m deep; fine green sand, pebbles and shells; det. M. Burton (R.N. CLXVII.V). USNM 43128, 63°51'-63°50'S/62°38'-62°35'W (USARP, R.V. "Eltanin", cruise 6, stn. 439), 09/I/1963, 128-165 m deep, det. V.M. Koltun. *M. gaussiana*, BMNH 1887.11.24.1, 74°30'S-175°E (Expedition Admiralty), 540 m deep, originally as *Esperella* sp., det. R. Kirkpatrick.

*Diagnosis:* The species is easily distinguished by the shape of its anisochelae-I and -II, which are almost arcuate on profile view, with very long and thin alae of the head.

*Description* emended from RIDLEY & DENDY (1887): The holotype of *E. lapidiformis* is massive, squarish, with rounded corners, like a water-worn boulder. Its dimensions are 131-88-69 mm. Texture is soft and fibrous, surface evenly microhispid with a thin and transparent membrane. Oscula consist of numerous short, wide, tubular processes, scattered over the upper end of the sponge. The walls of these tubes are thin and membranous, strengthened by very closely-placed subtylostyle





FIGS 43-54

*Mycale* (*M.*) *lapidiformis* (Ridley & Dendy, 1886). Holotype (BMNH 1887.5.2.160; figs 43-49). 43, overview of SEM stub showing abundance of sand grains. 44, terminations of subtylostyles. 45, frontal view of anisochela-I. Note very thin and long alae of the head and highly developed lateral alae of the foot. 46, bottom side view of the foot of anisochela-I. 47, frontal view of anisochela-III. Note shape largely comparable to that of anisochela-I (fig. 45). 48, frontal view of anisochela-3. Note presence of two spurs on foot. 49, unusual anisochela-III with very long and thin alae of the head. USNM 43128 (figs. 50-54). 50, heads of subtylostyles. 51, frontal view of anisochela-I. Note less developed lateral alae of the foot when compared to those of the holotype (fig. 45). 52, profile view of anisochela-II. Note shape highly comparable to that of anisochela-I (fig. 51). 53, frontal view of anisochela-III. Note presence of two spurs on foot. 54, unusually small anisochela-II. Compare with unusually large anisochela-III with a basal spur from holotype (fig. 49). Scales: fig. 43 = 500  $\mu$ m; fig. 44 = 30  $\mu$ m; figs. 45-47 and 49 = 10  $\mu$ m; fig. 48 = 5  $\mu$ m; fig. 50 = 50  $\mu$ m; fig. 51 = 20  $\mu$ m; figs. 52 and 54 = 10  $\mu$ m; fig. 53 = 5  $\mu$ m.



bundles which diverge in tufts when approaching the free edge, thus forming a slightly projecting fringe around the oscula. Colour in spirit is yellowish-grey.

The USNM specimen is 120-70-50 mm in dimensions (length, breadth, thickness). Its shape resemble that of a mango with a deep moss (~ 20 mm deep) making a longitudinal curve in one of its sides. It is only slightly compressible, with an evenly microhispid surface. Two small oscula are visible on the upper surface of the specimen, highly contracted (2 mm wide), which do not form tubular processes. The specimen is attached to a small basaltic boulder (70-50-30 mm, with some iron infiltration) and its colour in spirit varies from very light-yellowish-brown to slightly darker yellowish-brown.

The ectosomal skeleton of the holotype is composed of a palisade-like, dense side-by-side arrangement of subtylostyle tufts which are perpendicular to the surface. The apical termination of these subtylostyles projecting 110-220  $\mu\text{m}$  beyond the surface. On a transverse section the first 200  $\mu\text{m}$  are characterized by darker pigmentation and a dense layer of anisochelae and sediment grains. The tufts extend about 1000  $\mu\text{m}$  into the sponge, and a layer (~ 1000  $\mu\text{m}$  thick) of criss-crossing subtylostyles, many of them parallel to the surface (transverse to the tufts) start 400-550  $\mu\text{m}$  deep in the sponge. The choanosome is less spicularly dense than the ectosome, but is still characterized by great numbers of longitudinally running subtylostyle bundles (150-250  $\mu\text{m}$  thick), which diverge very-often, finally generating the abundant ectosomal tufts. Anisochelae and sediment grains (fig. 43) are abundant all over the choanosome, the former not organized in rosettes.

The USNM specimen presents the same skeletal pattern, but for the projecting subtylostyles which stick out more than 500  $\mu\text{m}$ . The few large sigmas observed were equally spread from the very surface to the deeper choanosome, where subtylostyle bundles were up to 1000  $\mu\text{m}$  thick at intersection points, and about 400  $\mu\text{m}$  thick on loose segments.

Spicules (micrometries see Table 2). Holotype. Megascleres: (Subtylo)styles (figs. 43-44), mostly straight, rarely slightly curved, with long, only very faintly constricted necks. Microscleres: Anisochelae-I (abundant; figs. 45-46), verging towards arcuate condition on profile view, head about 60% of shaft's height, foot relatively large. Alae of head very long, but very thin, all projecting towards the foot. Lateral alae of base projecting laterally. No plain foot, rather it is acute but with no projecting spur. Anisochelae-II (common; fig. 47), same as anisochelae-I, but smaller. Anisochelae-III (abundant; fig. 48-49), more typical shape. Head with two lateral alae largely attached to the shaft and a wide frontal one. Foot, small with spur-like projections running upward from top of frontal ala, and downwards from lower extremity of shaft. Rhaphids (very rare), smooth. USNM specimen. Megascleres: Subtylo(styles)(fig. 50), same as in holotype but seldom discretely polytylote, olive-like head more readily made out. Microscleres: Anisochelae-I (abundant; fig. 51), same as in holotype, but lateral alae of foot less developed. Anisochelae-II (common; fig. 52, 54), same as anisochelae-I, but smaller. Anisochelae-III (abundant; fig. 53), same as in holotype. Sigmas (uncommon), very large. Evenly curved, but short hooks suddenly bent. Trichodragmas (rare), rectangular, unevenly ended.



TABLE 2

Spicule micrometries of *Mycale* (*M.*) *lapidiformis* (Ridley & Dendy, 1886), *Mycale gaussiana* Hentschel, 1914 and *Mycale profunda* Koltun, 1964, partly from the literature, partly remeasured. Micrometries refer to minimum-mean-maximum. Unless otherwise stated, N = 20 for material presently remeasured.

	subtylostyles length X width	anisocheles -I/ -II/ -III	sigmas	rhapsids or trichodragmas
RIDLEY & DENDY, 1887 Holotype remeasured	900 X 20 583-698.8-767 X 15-17.6-19	94 (+ young ones) 76-87.3-96/ 44-57.3-70/ 29-34.1-43		r.44-74.8-88 (N = 7)
BMNH 1928.2.15.452 "Discovery" Exp. det. M. Burton	551-631.8-691 X 12-15.3-18	66-71.7-81/ 43-50.3-59/ 26-30.8-46	84-137 (N = 4)	t.59-67.9-81 X 4-7 r.55-67.5-83
USNM 43128 as <i>M. lapidiformis</i> det V.M. Koltun	799-883.4-950 X 19-23.0-26	79-88.4-100/ 52-58.4-69/ 32-36.2-39	70-185.4-204	t.42-48 (N = 3)
HENTSCHEL, 1914 <i>M. gaussiana</i> Holotype	720-808 X 18-20	49-79/ 27-31		t.37-50
BMNH 1887.11.24.1 as <i>M. gaussiana</i> det. R. Kirkpatrick	724-832.1-918 X 17-20.9-25	78-82.9-90/ 53-60.0-75/ 36-38.1-45		r.40 (N = 1)
<i>M. profunda</i> Koltun, 1964	780-890 X 15-23	57-74/ 34-39	108-136	

Remarks: The distinction between three "variable" categories and one "highly variable" category of anisocheles, is likely to be arbitrary. Figures 49 and 54 show two anisocheles which based on their overall shape and size would fit smoothly into the same category in the traditional approach to the taxonomy of *Mycale*. Nevertheless, emphasis is here shifted towards particular aspects of their morphology which suggest that one of them (fig. 49) belongs to category-III while the other (fig. 54) belongs to category-II.

The suggested synonymy of *M. gaussiana* with *M. (M.) lapidiformis* conforms to the implicit opinion of V.M. Koltun, who identified a "*gaussiana*"-like specimen as *M. lapidiformis* (USNM 43128, figs. 50-54). The fact that HENTSCHEL (1914) did not mention *M. (M.) lapidiformis*, despite their strikingly similar and peculiar anisocheles, points to the possibility that he overlooked the latter species when describing *M. gaussiana*. *Mycale profunda* was erected by KOLTUN (1964) on the basis of its large sigmas and slightly polytylote subtylostyles. This species is challenged here on the basis that the same characters are present in USNM 43128, identified by Koltun as *M. lapidiformis*. Large sigmas were also seen in low numbers in the "Discovery" specimen. Their instability is taken as supporting a hypothesis of intraspecific variability when the basal lateral-alae of anisocheles-I and -II are

described as further developed in *M. (M.) lapidiformis* when compared to *M. gaussiana*. The same applies, respectively, to the absent/unseen vs. rare trichodragmas.

So far there are only a few specimens described under either name, all from deep-water (128-3000 m deep), and from two contiguous areas of endemism, viz. the Magellan and Antarctic provinces. The close biogeographical affinity of both provinces [SARÀ *et al.*'s (1992) "Antarctic Faunistic Complex", which also includes most of the subantarctic islands; DESQUEYROUX-FAUNDEZ (1994)] is a further support to the hypothesis of conspecificity of the species discussed above.

*Mycale cylindrica* (Whitelegge, 1906) may be related to *M. (M.) lapidiformis* as suggested by WHITELEGGE (1906), but the synonymy is unlikely due to major skeletal and spicular differences, and largely discontinuous distribution. *M. cylindrica* was originally described with an axial/radial skeleton, megascleres only 200 µm long, as well as with only one, much smaller category of anisochelae (32 µm). An evaluation of the proper status of Whitelegge's species can not be undertaken here, as its type species was not examined, and an illustration of the spicule's geometry is absent from the original description.

The assignment of *M. (M.) lapidiformis* to the subgenus *Mycale* is tentative due to its unique ectosomal skeleton pattern. The absence of a tangential layer is the condition stressed as diagnostic for *Carmia* (see VAN SOEST, 1984; BERGQUIST & FROMONT, 1988), and also found in *Arenochalina*. Nevertheless, in the sense of TOPSENT (1924) the subgenus *Mycale* was recognized on the basis of its surface tufts rather than by its tangential skeleton (VAN SOEST, 1984). We are not suggesting that tangential ectosomal skeletons are not a good character, because they seem to be congruent with other trends (viz. presence of curved anisochelae-I, spurred anisochelae-III, pore-grooves and two size-classes of megascleres, see discussion below). But we hypothesize here that the loss/absence of a tangential ectosomal skeleton is likely to be homoplastic within the genus *Mycale*, as *M. (M.) lapidiformis*, and the subgenera *Carmia* and *Arenochalina* (all sharing the absence/loss of their ectosomal tangential skeletons), do not conform in most other morphological characters. We are here emphasizing the high spicular density of *M. (M.) lapidiformis*, its surface brushes and spurred anisochelae-III in assigning it to the subgenus *Mycale*.

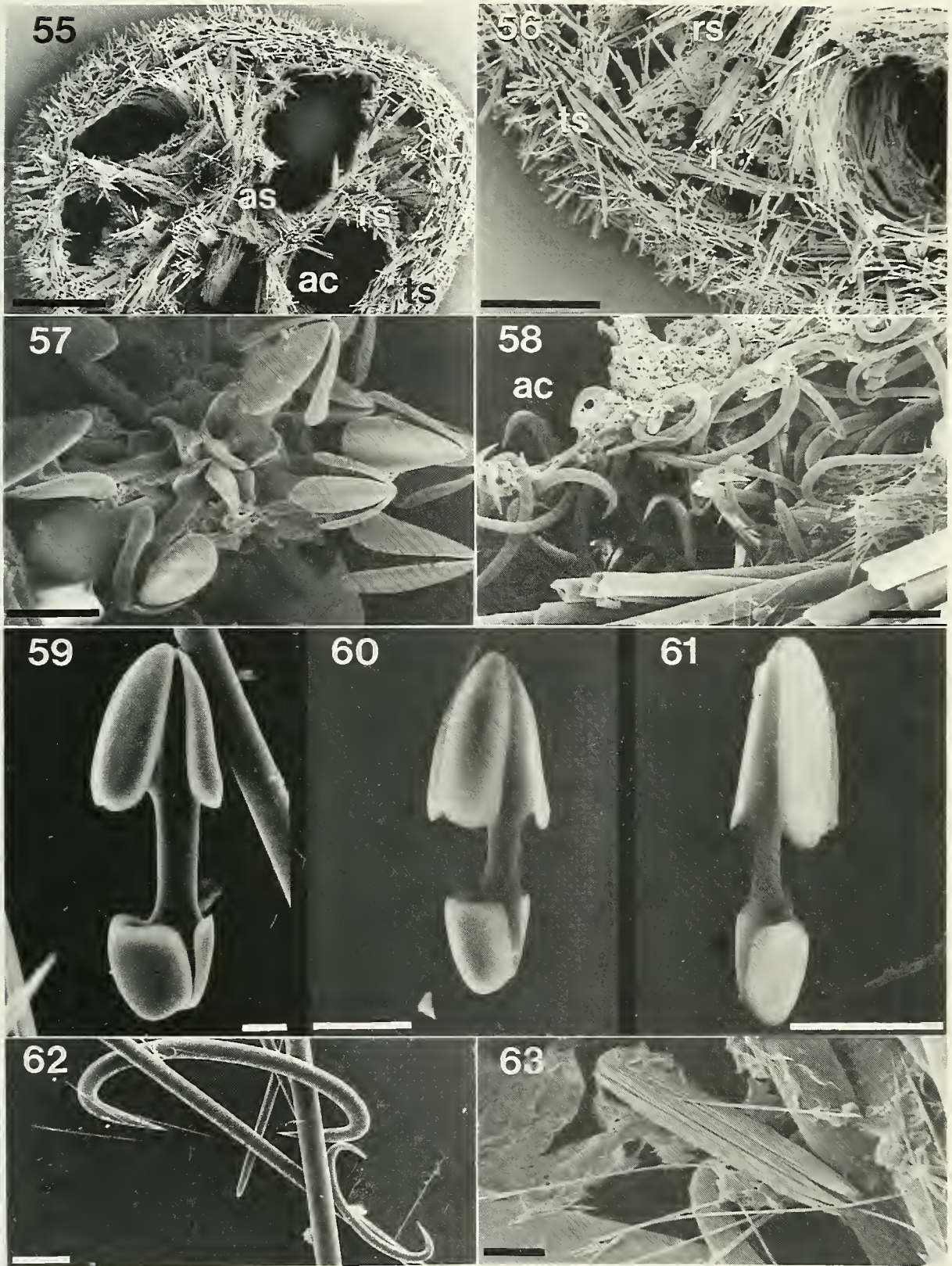
DE LAUBENFELS (1936) made *M. (M.) lapidiformis* the type of a new genus, *Mycalecarmia*, for species formerly assigned to *Mycale* but having a "rather less cavernous architecture than typical *Mycale*", and no sigmas and/or toxas. As stressed below, his adoption of DENDY's (1922) ideas of subdividing *Mycale* on the basis of categories of microscleres present are highly inconsistent with other shared traits among species, viz. ectosomal skeletons and shape of microscleres, and bound to be unnatural.

### ***Mycale (Mycale) quadripartita* Boury-Esnault, 1973**

*Mycale quadripartita* BOURY-ESNAULT, 1973: 278-279, fig. 31, pl. II.2.

Material studied: Holotype, MNHN.LBIM.NBE 1010, 13°18'S-38°42'W ("Calypso" Stn. 64), 45-48 m deep. Schizotype, UFRJPOR 3387. Additional material from the N Brazilian coast:





FIGS 55-63

*Mycale* (*M.*) *quadripartita* Boury-Esnault, 1973 (holotype, figs. 55-58 and 63; UFRJPOR 549, figs. 59-62). 55, transverse section showing main acquiferous channels (ac) running longitudinally, central axial skeleton (as), secondary radial skeleton (rs) and ectosomal tangential skeleton (ts). 56, brushes of the secondary radial skeleton (rs) supporting the ectosomal tangential skeleton (ts). Note abundance of rosettes (r). 57, rosette. 58, "bundle" of sigmas surrounding acquiferous channel (ac). 59, frontal view of anisochela-I. 60, frontal view of anisochela-II. 61, frontal view of anisochela-III. 62, sigmas-I, -II and -III. 63, trichodragma. Scales: fig. 55 = 1 mm; fig. 56 = 500  $\mu$ m; figs. 57-58 and 62 = 30  $\mu$ m; figs. 59-61 and 63 = 10  $\mu$ m.



UFRJPOR 549, 02°12'S-42°25'W ("N.O.A.S." Stn. 1817, off the coast of Maranhão), 60 m deep, 1968; UFRJPOR 608, ("N.O.A.S." Stn. 1882, off the coast of Pará), IV/1968; UFRJPOR 613, 00°23.0'S-47°16.1'W ("N.O.A.S." Stn. 1889, off the mouth of the Amazon), 31 m deep, 26/IV/1968; UFRJPOR 743, ("N.O.A.S." Stn. 1763, off the mouth of the Amazon), 23 m deep, 1967; UFRJPOR 948, 00°23.0'S-47°16.1'W ("N.O.A.S." Stn. 1889, off the mouth of the Amazon), 31 m deep, 26/IV/1968; UFRJPOR 960, ("N.O.A.S." Stn. 2012, off the coast of Amapá).

*Diagnosis:* *M. (M.) quadripartita* is a rather conspicuous sponge, characterized by its banana-shape (see below), four main acquiferous channels on transverse section and sigmas-I on the 200 µm range.

*Description* of the material collected by the Navio Oceanográfico Almirante Saldanha (N.O.A.S.): Specimens are cylindrical, fusiform, slightly bent (like a banana), small (1-3 cm long X 4-8 mm thick), firm, with an uneven surface. They are light yellowish-white (549, 613, 743), light yellowish-brown (608) or light gray (960) in alcohol. One specimen from sample 549 possesses the peduncle exhibited by the holotype.

The ectosomal skeleton is composed of a dense, mostly tangential, multilayer of subtylostyles (300-600 µm thick; fig. 55-56). Most spicules are perpendicularly disposed regarding the longitudinal axis of the sponge, but some criss-crossing pattern is also apparent. Spongin is not conspicuous, but an enormous amount of intermingled sigmas-II and -III is likely to play an important role in keeping the structure stable. A few isolated anisochelae-I can be seen on the inner parts of the tangential skeleton.

The choanosomal skeleton consists of a central, longitudinally-running bundle of subtylostyles, which is about 1 mm thick in its maximum diameter (fig. 55). This axial bundle contains a larger proportion of the larger subtylostyles. There is a secondary radial skeleton connecting the main axial bundle to the tangential ectosomal skeleton (fig. 55-56). Perpendicular tracts (100 µm wide) depart from the central axial bundle and split several times before reaching, and slightly trespassing (~100 µm) the ectosomal layer. A single tract might diverge enough to support 4 mm of tangential skeleton. Four or five, large (up to 2500 µm wide), longitudinal acquiferous channels run among the radial tracts. A few rosettes of anisochelae-I (170 µm wide; fig. 57) occur just below the tangential skeleton. Sigmas-I (not very common) are arranged parallel to the radial tracts, their hooks generally facing outwards. Extremely abundant, tightly packed sigmas-II and -III (not forming sigmodragmas), along with trichodragmas and anisochelae-II and -III are found among the radial diverging tracts and just below the ectosomal skeleton (fig. 58).

Spicules (micrometries see Table 3). Megascleres: Subtylostyles or subtylostrogyles, mostly straight, but some slightly bent or slightly sinuous occur. Fusiform, with elliptic head. Apex, mostly abruptly, sharply pointed or lanceolated. A trimodal length-distribution is scarcely made out, but plenty of intermediately-sized spicules occur. Microscleres: Anisochelae-I (fig. 59), straight shaft on profile view, frontal ala of the head forms larger angle with shaft than does the frontal ala of the base. Head about 40% microscelere length. All extremities of alae from head and foot roundish with no projections. Anisochelae-II (fig. 60), straight shaft on profile view, frontal ala of both head and foot form about the same angle with the shaft. Head about 50% of



microsclere length. Upper extremity of frontal ala of the foot might bear a central small roundish protuberance, all other extremities are roundish. Anisochelae-III (fig. 61), straight shaft on profile view, frontal ala of both head and base form about the same angle with the shaft. Head about 50% of microsclere length. Upper extremity of frontal ala of the base might bear a central small roundish protuberance, all other extremities are roundish. Besides getting smaller and smaller, anisochelae-I, -II and -III also present a gradient of width in frontal view, getting narrower and narrower, the smaller they are. Sigmas-I (fig. 62), s-shaped, abruptly bent, with very sharp, wedge-like hooks. Sigmas-II (fig. 62), s-shaped, abruptly bent, with sharp hooks. Sigmas-III (fig. 62), s-shaped, less abruptly bent, with sharp hooks. Trichodragmas (fig. 63).

TABLE 3

Spicule micrometries of *Mycale* (*M.*) *quadripartita* Boury-Esnault, 1973, partly from the literature, partly remeasured. Micrometries refer to minimum-mean-maximum. Unless otherwise stated, N = 20 for material presently remeasured.

	subtylostyles length X width	anisochelae -I/ -II/ -III	sigmas -I/ -II/ -III	trichodragmas
Boury-Esnault, 1973	444-1014 X 12-15	100-115/ 34-56/ not given	221-265/ 47-68	60-68
holotype remeasured	330-550-800 X 3.8-12.8-17.5	68.8-86.4-97.5/ 30-39.1-45/ 22.5-27.3-35	170-191.3-210/ 50-56.1-72.5/ 15-24.0-42.5	47.5-60.3-95
UFRJPOR 549	240-426.5-600 X 10-12.8-17.5	75-84.8-95/ 35-41.5-60/ 23.8-28.1-32.5	150-177.1-200/ 52.5-70.5-95/ 15-23.8-32.5	55-60.3-78.8
UFRJPOR 608	300-527.5-750 X 6.3-14.0-22.5	67.5-73.3-80/ 30-37.2-45/ 20-24.2-27.5	140-165-180/ 42.5-61.0-77.5/ 17.5-23.6-27.5	50-60.8-112.5
UFRJPOR 613	280-483-700 X 7.5-13.4-20	65-74.9-80/ 37.5-41.7-52.5/ 25-27.3-32.5	150-166-190/ 32.5-52.8-75/ 17.5-24-27.5	52.5-58.1-68.8
UFRJPOR 743	270-462.5-620 X 7.5-11.2-15	63.8-72.7-82.5/ 32.5-42.4-57.5/ 20-24.9-28.8	140-161.5-180/ 52.5-66.6-77.5/ 20-29.2-37.5	42.5-53.1-63.8
UFRJPOR 948	280-464.5-550 X 7.5-10.9-15	63.8-68.3-72.5/ 37.5-49.8-60/ 21.3-24.0-27.5	140-159.5-180/ 50-66.9-77.5/ 25-31.8-40	30-46.8-62.5
UFRJPOR 960	320-552.5-720 X 3.8-13.2-17.5	60-84.9-100/ 40-45.3-55/ 26.3-33.0-37.5	150-176-190/ 55-77.6-97.5/ 15-17.5	43.8-51.3-62.5

Remarks: *M. (M.) quadripartita* and *M. simonis* (Ridley & Dendy, 1886; holotype examined, BMNH 1887.5.2.163) from South Africa can be associated on the basis of the shape and skeletal arrangement of their sigmas-I [also conforming to the pattern observed in a few *Hamacantha* Gray, 1867, e.g. *H. popana* (De Laubenfels,

1935), see HAJDU, 1994]. The presence of an ectosomal reticulated skeleton, more robust anisochelae-I and -II, anisochelae-III with a digitiform process on the upper extremity of the frontal ala of its foot, and two categories of toxas, the smaller with spines, are some of the features which make *M. simonis* very distinct from *M. (M.) quadripartita*. For the present, phylogenetic relationships of this later species remain unresolved.

**Mycale (Mycale) thielei n.sp.**

? *Mycale* sp.; THIELE, 1905: 443, figs. 61a-d.

*Material studied*: Holotype, MHNG 972.235, Vald 15-2, 42°10'S-72°24'W (Quintupeu, Golfo de Ancud, Chile), 16/VII/1972, coll. C.A.Viviani, 15 m deep. Schizotypes: UFRJPOR 4234 and ZMA 10585. Paratypes: MHNG 971.184 (fragment under UFRJPOR 4239), Vald 41a, 42°53'S-73°40'W (Compu, Golfo de Ancud, Chile), 31/X/1971, coll. C.A. Viviani, 6-20 m deep; MHNG 972.236 (fragment under UFRJPOR 4238), Vald 64; MHNG 972.237, Vald 26 (both, 42°10'S-72°24'W; Quintupeu, Golfo de Ancud, Chile).

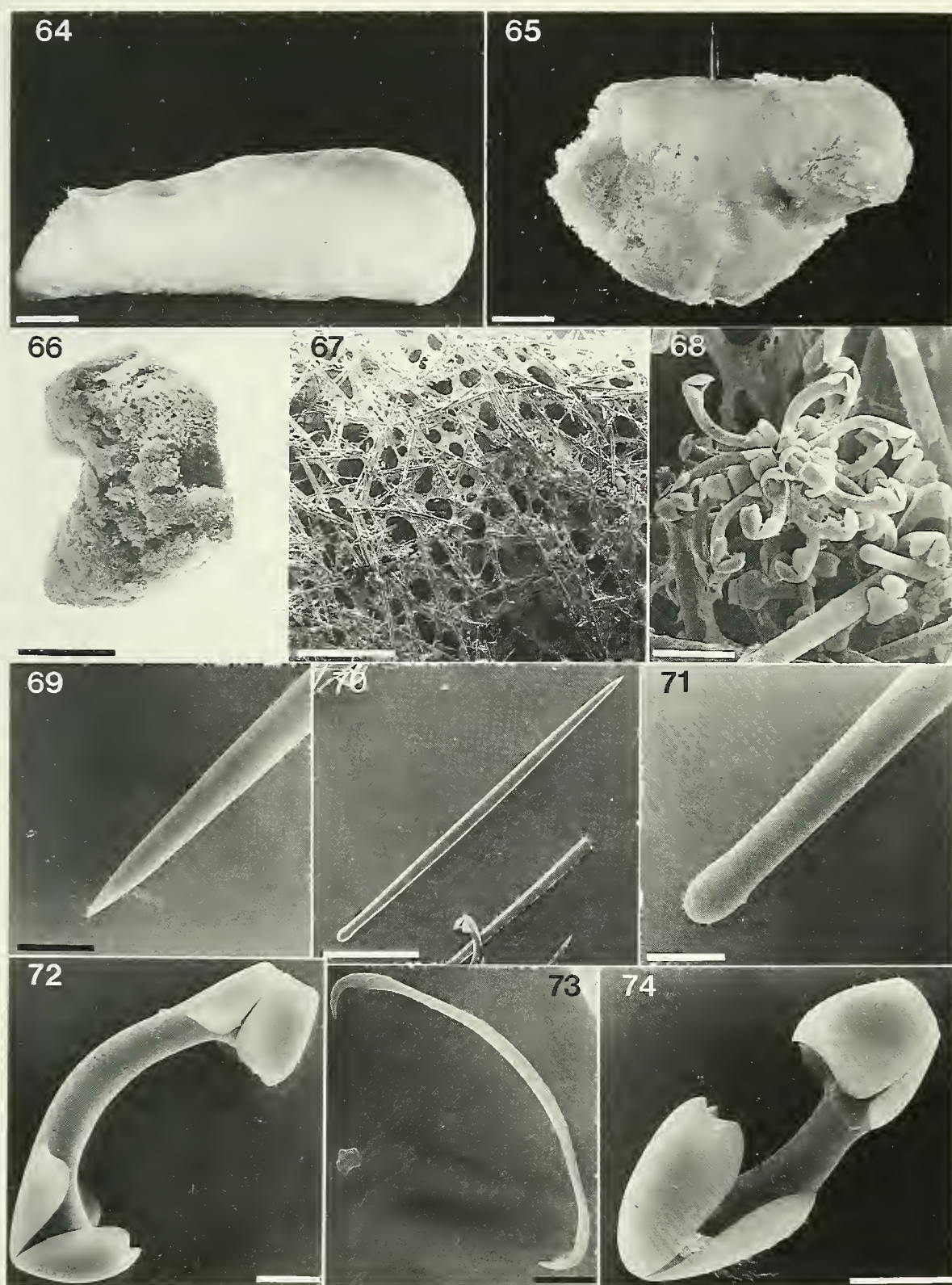
*Diagnosis*: The species is distinguished from other species belonging to the subgenus *Mycale* by a unique combination of characters. It is the only one possessing only one category of megascleres, anisochelae-I bearing a curved shaft and an "open-head" (large angle between the shaft and the frontal ala of the head), anisochelae-II either very rare or absent, and only one category of sigmas.

*Description*: The holotype is composed of two fragments. The largest one is regularly cylindrical, 112 mm high X 28 mm wide nearer to the base and 38 mm wide at the apical extremity (fig. 64). Its attachment base is missing. The smaller fragment has 54 mm X 25 mm in dimensions. Both have a smooth surface, firm consistency, no easily detachable surface peel as well as no pore grooves. Three apical openings (?oscula) are 2-3 mm wide. No aquiferous channels are conspicuous to the bare eye in the dense choanosome. Colour in alcohol is bright white. Paratypes are 46 mm X 23 mm X 29 mm large (MHNG 971.184; fig. 65), and 35 mm X 21 mm X 23 mm (fig. 66) and 28 mm X 11 mm X 11 mm (MHNG 972.236, two fragments; the latter enveloping a polychaete tube).

There is a confused tangentially arranged ectosomal skeleton 300-440 µm thick (fig. 67). The choanosomal skeleton is made of ramifying ascending tracts ending in brushes which lay side-by-side and support the surface skeleton. Ascending tracts are 80-100 µm thick just below the surface brushes, and 180-240 µm thick about 1.5 mm deep in the sponge. Rosettes of anisochelae-I (~ 140 µm in diameter; fig. 68) are abundant all over the sponge (including deep parts of the choanosome). Anisochelae-III and sigmas are very frequent all over the sponge, but sigmas are especially common surrounding the aquiferous channels.

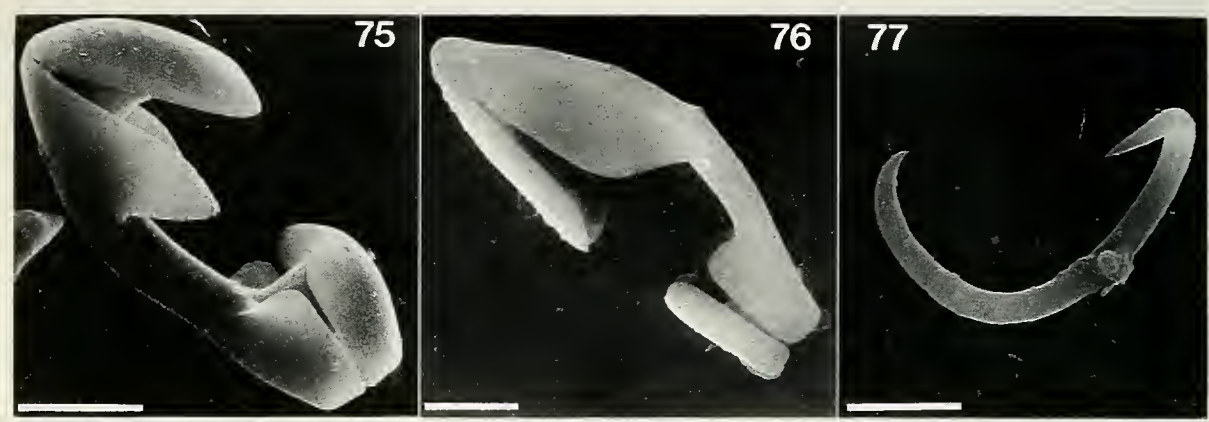
Spicules (micrometries see Table 4). Megascleres: Subtylostyles (fig. 69-71), smooth; fusiform, straight, thickest at middle part, ovoid head only very faintly marked, gradually tapering apical extremity. Microscleres: Anisochelae-I (very common; fig. 72), two extremities of about the same size (height and diameter), frontal tooth of the head forms a larger angle with the shaft than the one of the foot, tooth of the head might be slightly terminally invaginated, wide space between both terminations.





FIGS 64-74

*Mycale* (M.) *thielei* sp.n. (holotype, figs. 64, 67-77; paratypes, figs. 65-66). 64, holotype. 65, paratype MHNG 971.184. 66, paratype MHNG 972.236. 67, confused surface reticulation. 68, rosette. 69, apex of subtylostyle. 70, subtylostyle. 71, head of subtylostyle. 72, profile view of anisochela-I. 73, early developmental stage of anisochela-I with a sigmoid shape. 74, frontal view of anisochela-II.



FIGS 75-77

*Mycale* (M.) *thielei* sp.n. 75, profile view of anisochela-II. 76, profile view of anisochela-III. 77, sigma. Scales: figs. 64-66 = 1 cm; fig. 67 = 500  $\mu$ m; fig. 68 = 50  $\mu$ m; figs. 69 and 71 = 20  $\mu$ m; fig. 70 = 100  $\mu$ m; figs. 72-75 = 10  $\mu$ m; figs. 76 and 77 = 5  $\mu$ m.

Plenty of juvenile forms resemble sigmas with variable precision (fig. 73), and might be misleading in the cuts if not seen on profile view. Anisochelae-II (very rare; figs. 74-75), robust, head only slightly larger than foot and forming slightly larger angle with the curved shaft, tooth of the head slightly invaginated terminally, alae of the head tending to arcuate condition, small space between head and foot. Anisochelae-III (common; fig. 76), slender, head double height of foot, head and foot forming same small angle with the shaft, shaft slightly bent at middle part, where the alae of the head end. Sigmas (uncommon; fig. 77), s-shaped, sharp endings.

TABLE 4

Spicule micrometries of *Mycale* (M.) *thielei* n.sp. and Thiele's (1905) *Mycale* sp. Micrometries refer to minimum-mean-maximum. Unless otherwise stated, N = 20 for material presently remeasured.

	subtylostyles length X width	anisochelae -I/-II/-III	sigmas
holotype MHNG 972.235	421-470.6-494 X 14-16.0-18	64-68.6-74/ 33 (N = 1)/ 21-22.2-24	13-14-15
paratype MHNG 971.184	429-445.5-494 X 15-16.8-19	70-76.2-82/ not found/ 20-21.9-24	14-15-16
paratype MHNG 972.236	381-459.7-502 X 14-15.2-18	66-71.0-80/ 36 (N = 1)/ 20-21.8-23	13-15-16
paratype MHNG 972.237	429-450.2-486 X 13-14.4-16	57-69.3-74/ not found/ 16-19.5-22	13-16.6-19
THIELE, 1905 as <i>Mycale</i> sp.	370-400 X 13	50 (?)/ not given/ 20-22	15



*Etymology:* The species is named after Johannes Thiele who markedly contributed to the present knowledge of Chilean sponges.

*Remarks:* THIELE's (1905) *Mycale* sp. is only tentatively assigned to the present species as the specimen appears to be lost and no preparation by Thiele could be found in the Berlin Museum (D. Kühlmann, pers. comm.). Thiele's omission of the anisochelae-II is considered unimportant as it was found to be very rare, whereas the shape and size of other spicules conform well to those presently found. BURTON's (1934) opinion, followed by KOLTUN (1964), of its possible conspecificity with *M. (A.) magellanica* (Ridley, 1881; holotype examined here, BMNH 1879.12.27.21) is rejected as the latter possesses an ectosomal skeleton of reticulated spicule bundles and microscleres of distinct morphology - notably anisochelae-I with a shaft which is not curved as in *M. (M.) thielei* n.sp.. Moreover, *M. (A.) magellanica* is a well known dustbin species badly in need of a revision. Burton's decisions in lumping species are to be considered very cautiously in general (VAN SOEST, 1984; BERGQUIST & FROMONT, 1988).

#### KEY TO THE SPECIES OF *Mycale* (*Mycale*) OCCURRING IN SOUTH AMERICA

- |   |   |                              |
|---|---|------------------------------|
| 1 | Megascleres frequently larger than 600 µm. . . . .  | 2                            |
| - | Megascleres never (or very seldom) larger than 600 µm. . . . .  | 4                            |
| 2 | Sigmas common. . . . .  | 3                            |
| - | Sigmas absent or very rare; anisochelae-I with very long and thin alae<br>. . . . . <i>M. (M.) lapidiformis</i>   |                              |
| 3 | Three categories of sigmas; sigmas-I can be larger than 100 µm;<br>banana-shaped; no pore-grooves. . . . .  | <i>M. (M.) quadripartita</i> |
| - | One category of sigmas; always smaller than 50 µm; with pore-grooves<br>. . . . . <i>M. (M.) arenaria</i>   |                              |
| 4 | Shaft of anisochelae-I markedly curved on profile view. . . . .   | 5                            |
| - | Shaft of anisochelae-I straight or slightly bent; trichodragmas very<br>common. . . . . <i>M. (M.) laevis</i>   |                              |
| 5 | With sigmas. . . . .  | 6                            |
| - | No sigmas. . . . . <i>M. (M.) doellojuradoi</i>   |                              |
| 6 | Anisochelae-I never larger than 70 µm. . . . .  | 7                            |
| - | Anisochelae-I larger than 70 µm. . . . . <i>M. (M.) thielei</i> n.sp.   |                              |
| 7 | One category of megascleres; anisochelae-I smaller than 50 µm<br>. . . . . <i>M. (M.) beatrizae</i> n.sp.   |                              |
| - | Choanosomal-megascleres straight and larger, ectosomal-megascleres<br>curved and smaller; anisochelae-I larger than 50 µm. . . . . <i>M. (M.) darwini</i> n.sp. |                              |

#### DISCUSSION

##### UNCERTAIN RECORDS

CUARTAS (1992) reported the occurrence of *M. (M.) trichela* Lévi, 1963 for the Argentinian Coast off Mar del Plata, stressing that the slightly smaller dimension

of the subtylostyles in her specimen (424-600/ 15 vs. 625-725/ 20  $\mu\text{m}$  in the holotype) was not enough to overrule the hypothesis of conspecificity with the type specimen from South Africa. The occurrence of only two categories of anisochelae in the Argentinian specimen as compared to three categories in the type was overlooked by CUARTAS (1992).

We have examined the holotype of the species (MNHN-LBIM-D.CL. 471) and found differences greater than expected relative to the Argentinian record. Notably, the shape of the anisochelae-I in *M. (M.) trichela* approaches that described by LÉVI (1963) for *M. (M.) sulcata* Hentschel, 1911 [= *M. (M.) darwini* n.sp. (figs. 15-16), *M. (M.) doellojuradoi* (figs. 24-25) and *M. (M.) thielei* (fig. 72)]. The possibility of changed labels is discarded as megascleres are in the 600  $\mu\text{m}$  range and no raphides or sigmas were seen, thus conforming to LÉVI's (1963) original description of *M. (M.) trichela*. The possibility of contamination from *M. (M.) sulcata* seems also unlikely as the anisochelae-I found by us in *M. (M.) trichela* are larger (75  $\mu\text{m}$ ) than those reported for the former species by LÉVI (1963; 46-52  $\mu\text{m}$ ), and were seen forming rosettes, which is taken as indicative of their autochthonous origin. Such anisochelae are markedly distinct from those figured by CUARTAS (1992), thus suggesting that the Argentinian specimen is probably only distantly related to *M. (M.) trichela*. The status of the former shall remain unresolved until some future revision.

#### AN OVERVIEW OF THE SYSTEMATICS OF *Mycale*

Traditionally, decisions on the hierarchic level of taxa have been influenced by both the observable amount of apomorphy and the postulated size of an assemblage (HENNIG, 1966). The genus *Mycale* Gray, 1867 is a typical example of a taxonomic assemblage that has been causing discomfort. More than a 150 species and varieties of *Mycale* are known (DOUMENC & LÉVI, 1987), which unlike the ones of most other large genera of sponges (notably *Haliclona* Grant, 1835), possess a diverse set of morphological characters of great disparity, which allows a relatively easier recognition of species.

The idea that several groups can be recognized within the genus *Mycale* Gray, 1867 (sensu VAN SOEST, 1984; WIEDENMAYER, 1989) is a concept as old as the genus itself, as GRAY (1867) erected five different genera for sponges sharing a comparable set of spicules (viz. *Mycale*, *Aegogropila*, *Grapelia*, *Carmia* and *Corybas*) and distinguished from each other in only minor morphological features. Owing to the incompleteness of several of the earlier species descriptions, notably in the overlooking of microscleire categories (HENTSCHEL, 1913; TOPSENT, 1924; DOUMENC & LÉVI, 1987), a multitude of synonymous species arose [see synonymy of *M. (Aegogropila) contarenii* (Von Martens, 1824) in TOPSENT (1924)]. Likewise, many genera were erected on the basis of supposed differences of undetermined phylogenetic consistency, viz. *Gomphostegia* Topsent, 1896; *Oxycarmia* De Laubenfels, 1954; *Parisociella* Burton, 1952; *Protoesperia* Czerniavsky, 1878;



*Sceptrospongia* Burton, 1928 (see suggested list of synonyms of *Mycale* in WIEDENMAYER, 1989). Decisions to lump taxa, when based solely on the poor available descriptions, were also bound to be extreme [e.g. TOPSENT's (1924) criticism of VOSMAER & PEKELHARING's (1898) synonymy of *Esperella aegogropila* (Johnston, 1842; = *M. (A.) contarenii*, sensu TOPSENT (l.c.))].

Three major attempts at subdividing the genus *Mycale* occur in the literature. DENDY (1922) suggested that the absence/presence of some microsclere categories could serve as satisfactory diagnostic features. Despite the fact that TOPSENT (1924) discarded DENDY's (1922) suggestion, maintaining that microsclere categories cut right through seemingly very closely related species, DE LAUBENFELS (1936), nevertheless, formally proposed a subdivision of *Mycale* (viz. *Mycale*, with sigmas but no toxas; *Carmia*, with toxas; *Mycalecarmia*, no sigmas and no toxas) which strictly agreed with the ideas expressed by DENDY (1922). This was a controversial move that generated a classification which has been heavily criticized and is not used today (VAN SOEST, 1984; DOUMENC & LÉVI, 1987).

A second major attempt was based on the arrangement of the ectosomal skeleton (TOPSENT, 1924). This system has gained support with recent authors (VAN SOEST, 1984; BERGQUIST & FROMONT, 1988; WIEDENMAYER, 1989) in spite of being flawed in the same aspects as that of DENDY (1922) and DE LAUBENFELS (1936), in that no outgroup comparison was performed prior to establishing the supposedly derived condition of ectosomal skeleton patterns. Additionally, both schemes match the Aristotelian A/not-A classification, which has extreme logical shortcomings and has been severely criticized in the recent theoretical literature on systematics (see VAN SOEST, 1990 for examples with sponges).

BERGQUIST & FROMONT (1988) decided that these assemblages, of questionable monophyly, should be raised to generic rank "to maintain uniformity", defending this move by the observation that characters diagnosing the subgenera of *Mycale* sensu VAN SOEST (1984) were the same used to diagnose genera in other familial assemblages. This decision is based on two unsustainable assumptions, viz 1. that taxa of same rank but in different assemblages can be diagnosed by the same characters [the basis of DE LAUBENFEL's (1936) controversial classification of families and genera], and 2. that taxa of other assemblages are properly (phylogenetically) classified. Before a phylogenetic classification of *Mycale* can be established we first need to know confidently the allocation of species to different species-groups within *Mycale* (which has not yet been done extensively), and which homologous characters corroborate phylogenetically sound taxa. Raising the status of such assemblages in the classification hierarchy without the proposition of any empirical support to do so is premature (especially if their monophyly is not firmly established, as in this case). Keeping these names at subgeneric rank, however, avoids unnecessary confusion among non-specialists (e.g. natural-products chemists, community ecologists, etc) in the event that the taxonomic allocations of the species may change after future systematic studies.

The third major attempt was introduced by HENTSCHEL (1913) and further developed by DOUMENC & LÉVI (1987) into a statistical evaluation of micrometric features of the anisochelae-I and some spicular micrometric ratios. Unfortunately DOUMENC & LÉVI's approach is limited by some poorer earlier descriptions and the restriction to the ranges of shapes of the anisochelae-I. Similarly, as in both former approaches in subdividing *Mycale*, the absence of outgroup comparison renders their results of doubtful value from a phylogenetic perspective. Nevertheless, the ideas behind their method are considered a major step towards a morphological phylogenetic classification of *Mycale*. RIDLEY & DENDY (1887), DENDY (1921), TOPSENT (1924, to a certain extent), DOUMENC & LÉVI (1987) and HAJDU *et al.* (1994a), all regard spicular morphological microfeatures as a trustworthy primary set of characters. This is based on the assumption that such characters are likely to have a very low adaptive value, thus reflecting phylogenetic constraints rather than adaptive pressures (Darwin Principle; MAYR, 1979; WHEELER, 1986).

#### MONOPHYLY AND AFFINITIES OF *Mycale* (*Mycale*)

The only test considered to be a valid check on conjectures of homology is that of congruence of characters (PINNA, 1991). Yet it is clear that in regard to *Mycale* this procedure has not been applied very often. From our preliminary survey of the genus, it is apparent that species classified under *M.* (*Grapelia*) (see VACELET *et al.*, 1976) can possess a confused tangential ectosomal skeleton comparable to the one in *M.* (*Mycale*) (present observations on BMNH.1934.11.20.94, Durban, South Africa, det. M. Burton as *M. parasitica*).

The relationship between both subgenera *Mycale* and *Grapelia* is additionally corroborated by two underlying synapomorphies, the presence of markedly curved anisochelae-I (on profile view) and the presence of basally-spurred anisochelae-III (both present in all species of *Grapelia*). Still, the absence of toxas is shared between them, and with subgenus *Arenochalina*. The widespread occurrence of toxas in subgenera *Aegogropila* and *Carmia*, and in the sister-family Hamacanthidae, makes it likely that the absence is derived (i.e. secondary loss).

Another character which seems to be restricted to the subgenus *Mycale*, although absent from several species, is the presence of two categories of megascleres. Ectosomal specialization in the form of additional megasclere categories present is a character occurring very seldom in the Mycalina (*Coelodischela* Vacelet *et al.*, 1976 and a doubtfully assigned genus, *Philyctaenopora* Topsent, 1904, see HAJDU *et al.*, 1994a) and here considered as derived within the subgenus *Mycale*.

BERGQUIST & FROMONT (1988) suggested the use of pore-grooves as an additional underlying synapomorphic character for *Mycale* (treated as a subgenus here). Although more than thirty species are known with an ectosomal skeleton conforming to the densely tangential pattern of *M.* (*Mycale*), less than ten have pore-grooves reported [only *M.* (*M.*) *arenaria* nom. nov. and *M.* (*M.*) *darwini* n.sp. possess them from the ones described above], which exemplifies the sort of problems encountered with when attempting a phylogenetic revision of *Mycale*.



## CLADISTIC ANALYSIS

Following here is a list of anatomical characters, and their states, used to assess phylogenetic relationships within *Mycale* and the Mycalidae (see table 5). Characters were polarized using the family Desmacellidae as an outgroup. *Hamacantha* Gray, 1867 was treated as part of the ingroup to check whether or not the outcome of the analysis would support its current interpretation as sister-group of the Mycalidae. Species of *Esperiopsis* Carter, 1882 were split into those conforming to *E. villosa* (Carter, 1874; the type species of the genus) and those conforming to *E. fucorum* (Esper, 1794), respectively named *Esperiopsis* 1 and *Esperiopsis* 2. This is in agreement with opinions expressed in the taxonomic literature which identify distinct lineages within *Esperiopsis* (BERGQUIST & FROMONT, 1988; HOOPER & LÉVI, 1989), and opinions from the general systematics literature regarding the coding of polymorphic taxa (e.g. NIXON & DAVIS, 1991). Following the same line of reasoning, *Grapelia* was split into two components to account for its apparent ectosomal skeleton polymorphism (EH, pers. obs.).

TABLE 5

Matrix of species by morphological characters used to assess relationships within *Mycale* and the Mycalidae. Refer to the text for description of characters and for explanation of reasons for using the present selection of taxa.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>M. (Mycale)</i>	1	1	1	2	0	2	2	0	0	1	1	0	0	1	0
<i>M. (Grapelia)</i> 1	1	1	1	2	0	2	0	1	1	1	2	0	1	0	0
<i>M. (Grapelia)</i> 2	1	1	1	1/3	0	2	0	1	1	1	2	0	1	0	0
<i>M. (Aegogropila)</i>	1	0	0	1/3	1	2	0	0	0	1	0	0	1	0	0
<i>M. (Paresperella)</i>	0	0	0	1/3	1	2	1	0	0	1	0	1	1	0	0
<i>M. (Carmia)</i>	1	0	0	0	1	2	0	0	0	1	0	0	1	0	0
<i>M. (Arenochalina)</i>	0	0	0	0	0	2	0	0	0	1	0	0	2	0	0
<i>Esperiopsis</i> 1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0
<i>Esperiopsis</i> 2	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
<i>Hamacantha</i>	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1
Desmacellidae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

Character 1: Three categories of chelae - 0. absent, 1. present. Neither *Hamacantha* nor Desmacellidae possess chelae, what makes the possession derived within the clade analysed. The occurrence of three categories of chelae outside the Mycalidae is unknown to the authors.

Character 2: Anisochelae-I with shaft markedly curved on profile view - 0. absent, 1. present. This shape of anisochela is described above from *M. (M.) arenaria* nom. nov., *M. (M.) beatrizae* n. sp., *M. (M.) darwini* n. sp., *M. (M.) doellojuradoi* and *M. (M.) thielei* n. sp., and is also known from several other

species belonging to the subgenus *Mycale* [e.g. *M. (M.) paschalis*, *M. (M.) sulcata*, *M. (M.) trichela*, see above]. All species of subgenus *Grapelia* possess anisochelae-I with a markedly curved shaft.

Character 3: Anisochelae-III with a basal spur-like projection - 0. absent, 1. present. This condition is described above from *M. (M.) arenaria* nom. nov., *M. (M.) darwini* n. sp. and *M. (M.) laevis*, and is known from several other species within subgenera *Mycale* [e.g. *M. (M.) anisochela* Lévi, 1963 and *M. (M.) massa* (Schmidt, 1862), see HAJDU & BOURY-ESNAULT (1991)] and *Grapelia* (all species).

Character 4: Ectosomal skeleton - 0. absent, 1. reticulated, 2. confused, 3. homoplastic reticulation. HOOPER *et al.* (1992) define *Desmacella* Schmidt, 1870, *Microtylostylifer* Dendy, 1924 and *Neofibularia* Hechtel, 1965 with tangential ectosomal skeletons. The patterns observed in the Desmacellidae are here interpreted as distinct from those of *Hamacantha* and the subgenera of *Mycale*.

Character 5: Toxa - 0. absent, 1. present. This is a character widespread in poecilosclerid and haplosclerid sponges (VAN SOEST, 1991; HAJDU *et al.*, 1994a, b), which is likely to have been switched-off and -on again several times as suggested by the patchy occurrence of toxa throughout variously related assemblages within both orders. Each event of switching-on or -off can be separately quoted as derived after mapped on the cladogram.

Character 6: Basic shape of chela - 0. no chelae, 1. isochelae, 2. anisochelae. Although chelae were recently postulated as an additional underlying synapomorphy for both orders Haplosclerida and Poecilosclerida (HAJDU *et al.*, 1994b), their absence from families Desmacellidae and Hamacanthidae turns their occurrence in the Mycalidae into a likely derived switch-on.

Character 7: Two categories of megascleres - 0. absent, 1. rare, 2. common. The occurrence of this character is very restricted in the Mycalidae. It is common within the subgenus *Mycale* [see *M. (M.) arenaria* nom. nov. and *M. (M.) darwini* n.sp. above], and known from only one species of *Paresperella* so far, viz. *M. (P.) levii* (Uriz, 1987).

Character 8: Unguiferate anisochelae-I - 0. absent, 1. present. This is a synapomorphic character for the subgenus *Grapelia* (see fig. 5 in HAJDU *et al.*, 1994a).

Character 9: Unguiferate anisochelae-II - 0. absent, 1. present. This is another synapomorphic character for *Grapelia* (see fig. 31c in VACELET *et al.*, 1976).

Character 10: Two categories of rosettes - 0. absent, 1. rare, 2. widespread. Rosettes are formed by both anisochelae-I and -II in all species of *Grapelia*, and in *M. (M.) myriasclera* Lévi & Lévi, 1983 (holotype reexamined, MNHN D.CL 2966).

Character 11: Serrated sigmas - 0. absent, 1. present. This character is autapomorphic for the subgenus *Paresperella* (VAN SOEST, 1984; BERGQUIST & FROMONT, 1988).

Character 12: Rosettes - 0. absent, 1. present. Rosettes are known from *Cornulotrocha* Topsent, 1927, *Iophon*, *Hamacantha*, *Esperiopsis* and *Mycale* (HAJDU, 1994). The first two taxa are only very distantly related to the clade in study - they belong to the suborder Microcionina - and are left out of this analysis. The



occurrence of rosettes in the other three taxa is here treated as homologous. This interpretation minimizes parallel developments and maximizes subsequent losses, being in accordance with SLUYS' (1989) and PINNA's (1991) suggestions regarding the coding of seemingly nonuniversally derived characters.

Character 13: Length of megascleres - 0. can be large ( $> 800 \mu\text{m}$ ), 1. can be medium ( $> 400 \mu\text{m}$ ), 2. small ( $< 300 \mu\text{m}$ ). The ability to build large megascleres is widespread within poecilosclerid sponges. We have arbitrarily divided the taxa that do not produce large megascleres into those producing medium sized ones ( $> 400$  but  $< 700 \mu\text{m}$ ) and those producing only comparatively small ones ( $< 300 \mu\text{m}$ ), in order to observe possible trends in the loss/switch-off of the ability to build large megascleres.

Character 14: Pore-grooves - 0. absent, 1. present. Pore-grooves were regarded by BERGQUIST & FROMONT (1988) to constitute an additional diagnostic character for the subgenus *Mycale*. In spite of their restricted distribution within the subgenus, their absence from any other closely related lineage seems to indicate their derived condition at this level of the taxonomic hierarchy. The autapomorphic condition of this character for the subgenus *Mycale*, as suggested by BERGQUIST & FROMONT (1988) and followed here, will only be tested however, after phylogenetic relationships within the subgenus have been analysed.

Character 15: Diancistras - 0. absent, 1. present. These are synapomorphic for the genus *Hamacantha* (HAJDU, 1994).

Figure 78 shows the cladogram resulting from analysing the data-matrix (Table 5) with PAUP. All characters were treated as unordered and polarized against the Desmacellidae. Quoting the ectosomal reticulations of *M. (Aegogropila)*, *M. (Grapelia)* and *M. (Paresperella)* as homologous to that of *Hamacantha* (Table 5, char. 4, state 1) yields 6 equally parsimonious trees. The majority-rule consensus of these trees keeps the sistergroup relationship of subgenera *Mycale* and *Grapelia* with a 100% support, but brings both *Esperiopsis* 1 and 2 within the genus *Mycale* (83% support, 5 out of 6 possible trees). An alternative solution is here tentatively advanced, which consists of quoting them as analogous (Table 5, char. 4, state 3 as opposed to state 1). This move is based on the widespread recognition that *Mycale* and *Hamacantha* belong to distinct families (e.g. TOPSENT, 1928; HOOPER *et al.*, 1992; HAJDU, 1994; HAJDU *et al.*, 1994a). The sistergroup relationship of both families (HAJDU, 1994) does not prevent *Hamacantha* to be more than two nodes away from subgenera *Aegogropila* and *Paresperella*, which is sufficient to regard their shared ectosomal reticulation as homoplastic (MADDISON *et al.*, 1984). The cladogram obtained in this way (fig. 78) is one of the six equally more parsimonious solutions found by PAUP if all four taxa are coded the same (char. 4, state 1).

This cladogram (fig. 78) is to be treated as a working hypothesis, as we presently have only a shortage of morphological data available for the analysis. Our recent efforts towards precisely describing species of *M. (Mycale)*, coupled with a preliminary check on material belonging to *M. (Grapelia)*, has yielded substantial

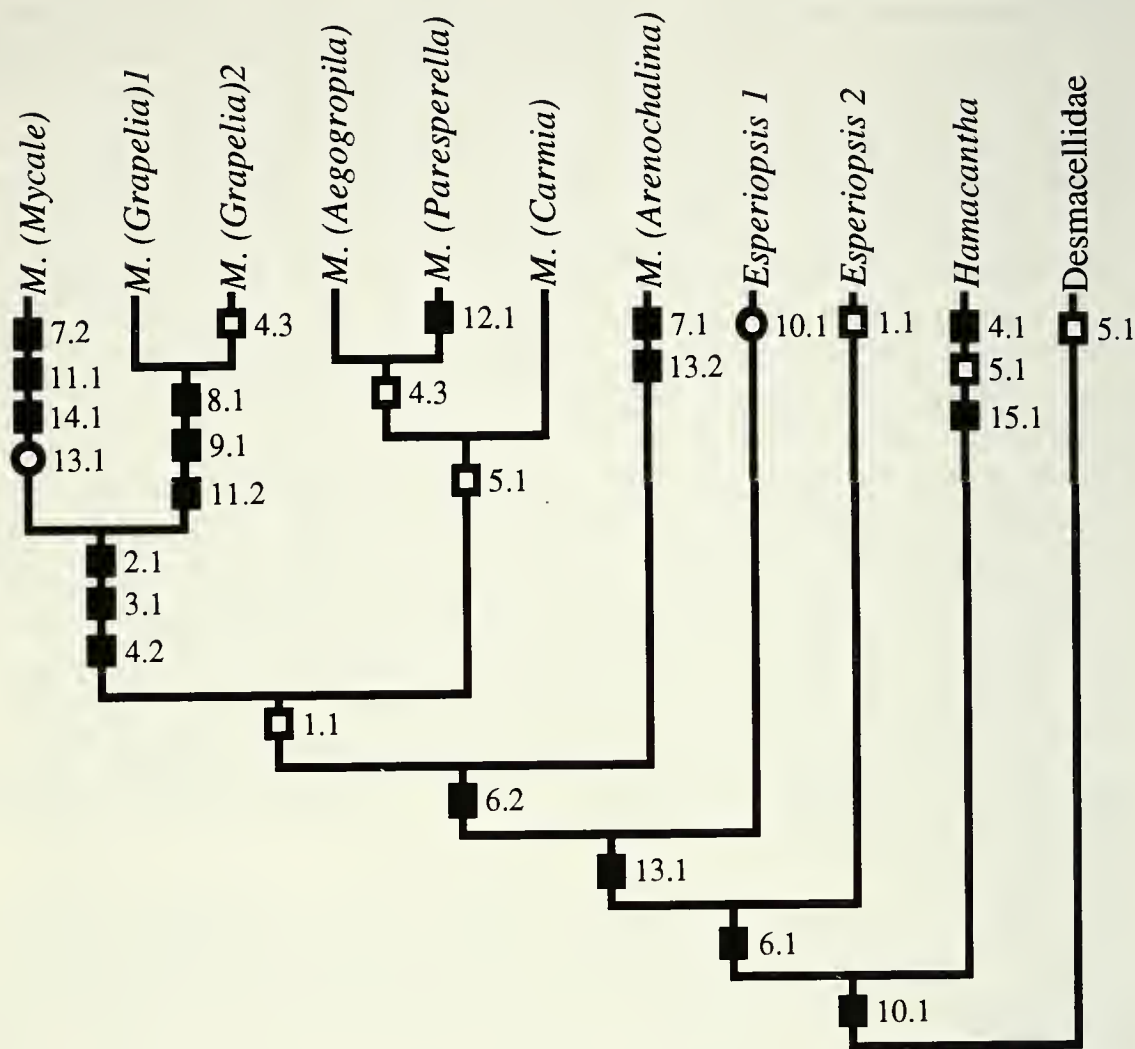


FIG. 78

Unique most parsimonious cladogram (tree length = 27, CI = 0.778) obtained by analysing the matrix in Table 5 with PAUP 3.0. All characters treated as unordered. ■ = synapomorphies, □ = parallel developments, ○ = reversals.

support for the monophyly of both assemblages as well as for their sistergroup relationship. It is to be expected that detailed study, especially of microsclere morphology, will considerably change relationships found for the other subgenera of *Mycale*. The paraphyletic condition of *Esperioipsis* also needs to be verified by a detailed character analysis of its constituent species.

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